THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR   Samuel J. Barry

TITLE OF THESIS   Mark-Recapture Estimates for An

Age-Structured, Time-Dependent

Population

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED   Spring 1982

THE UNIVERSITY OF ALBERTA

Mark-Recapture Estimates for An Age-Structured,

Time-Dependent Population

by

Samuel J. Barry

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Statistics and Applied Probability

EDMONTON, ALBERTA

Spring 1982

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and
recommend to the Faculty of Graduate Studies and Research,
for acceptance, a thesis entitled Mark-Recapture Estimates
for An Age-Structured, Time-Dependent Population submitted
by Samuel J. Barry in partial fulfilment of the requirements
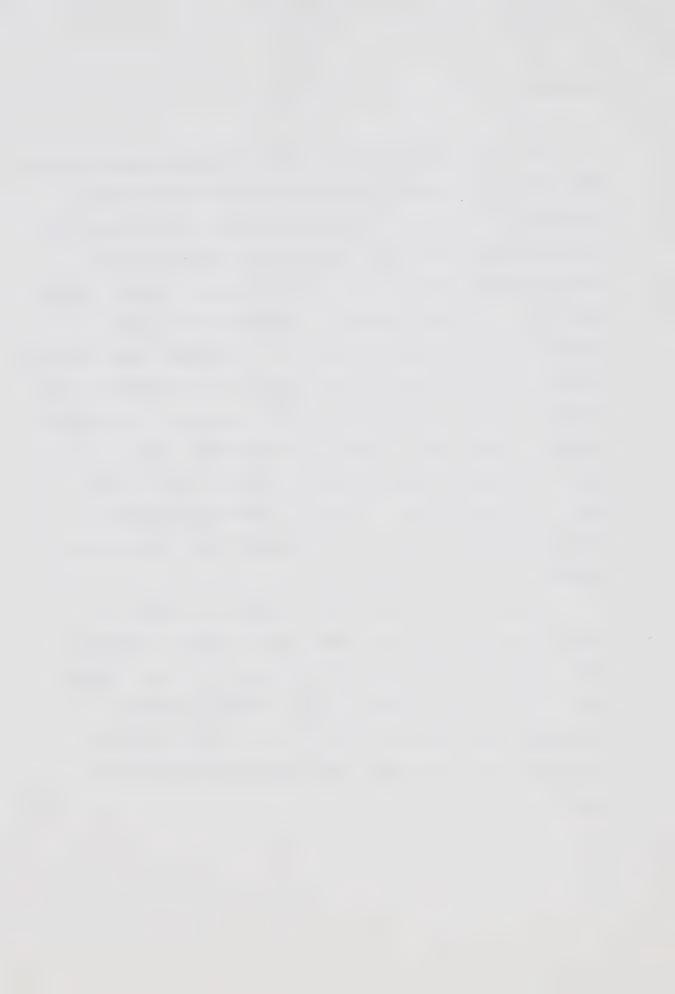for the degree of Master of Science.

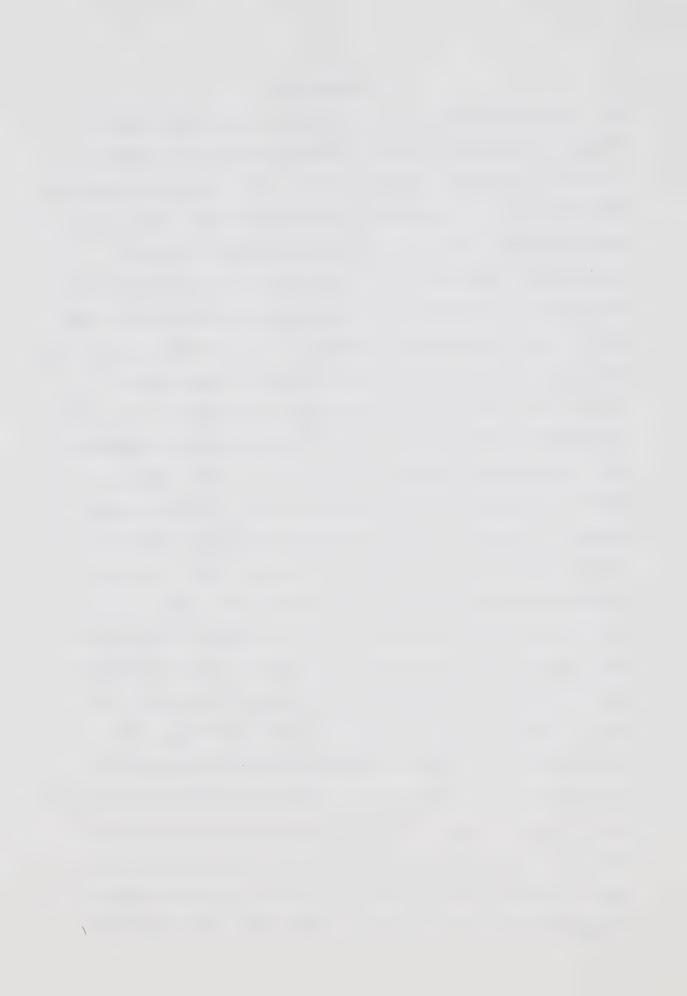To my best friend, Catherine McCune-Barry

Abstract

The Jolly-Seber method of analysing mark-recapture data
obtained from a simple homogeneous type of population is
extended to allow for some peculiarities to be present in
the population. The type of population considered is
non-homogeneous, consisting of only two age classes, young
and adult. The young require a fixed number of years, r, in
which to mature to adult status. It is assumed that only the
young of the year and the mature adults are catchable, the
subadults, for one reason or another, are not. This analysis
assigns to the young a probability that they survive the r
years to maturity and a different probability that the
adults survive one year intervals. Maximum likelihood
estimates for population size parameters and the survival
probabilities are provided.

The estimation equations are applied to a set of
capture-recapture data obtained from a colony of Pacific
brant (*Branta bernicla nigricans*) breeding in the Anderson
River Delta in the Canadian arctic. These data were
collected from 1959 to 1979 by Dr. T. W. Barry of the
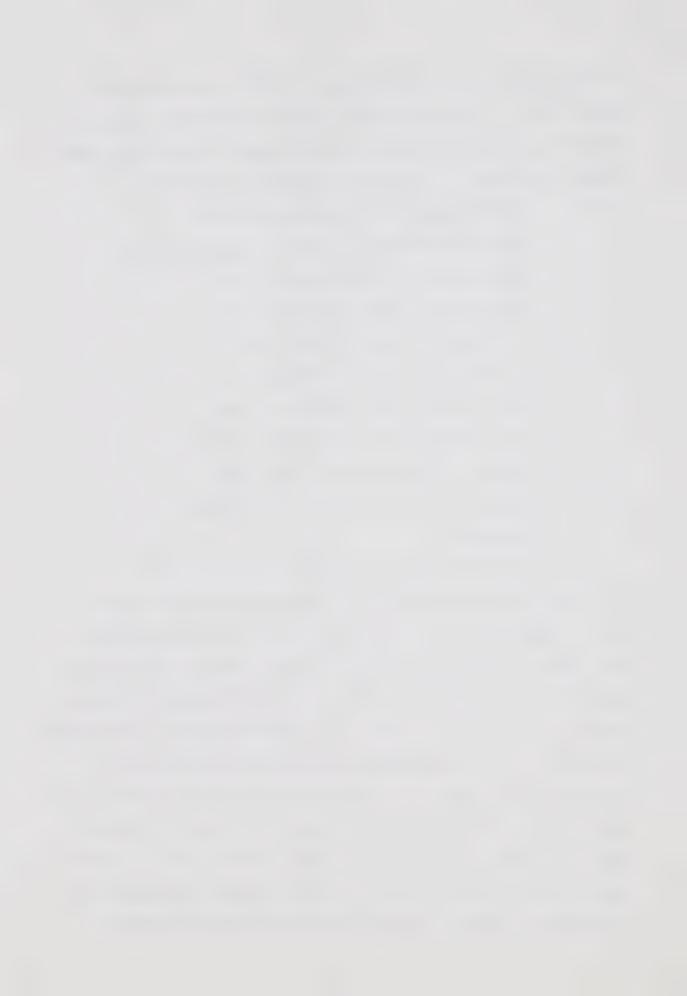Canadian Wildlife Service, with the assistance of the
author.

Introduction

For the past several years concern has been mounting for a
population of Pacific brant (*Branta bernicla nigricans*)
(Pacific Waterfowl Flyway Council, 1978) wintering along the
west coast of this continent. During the past twenty years
the wintering flocks of brant have dwindled in their
traditional areas along the coast from British Columbia to
California. Government agencies managing the Pacific Flyway
have noted a synchronous increase in brant numbers along the
Baja coast of Mexico (Pacific Waterfowl Flyway Council,
1978). With this growing concentration of geese in one area
the potential for greater exploitation by hunters becomes a
real and serious problem. It is also not clear whether this
shift is caused by brant abandoning their northern haunts in
favour of southern areas or whether the overall population
is experiencing actual numerical changes among its many
breeding subpopulations. Another matter of concern is the
continuing human encroachment into the coastal habitat of
this species, a pattern which may simply force the geese to
move out or else threatens their primary food source, the
beds of brackish water eelgrass (*Zostera marina*). The
transportation of heavy oil along the west coast and the
inevitable future production of arctic oil and gas will most
likely have a drastic effect on the wintering birds and
their habitat and on the breeding, molting, and staging
areas along the arctic coast. To alleviate these concerns a
management plan for the Pacific Brant has been formulated

(Pacific Waterfowl Flyway Council, 1978), setting forth
objectives for increasing the numbers and habitat and
adjusting the distribution of this goose. In meeting these
objectives there is one major obstacle to overcome:

> The management of a species rests
> upon the data base, and it, unfortunately,
> contains many serious gaps. The
> more serious deficiencies concern
> the amount of habitat and how it
> is changing, and the distribution,
> survival and recruitment of brant
> on a subpopulation-by-subpopulation
> basis. These gaps must be closed
> rapidly to provide for well founded
> management.
>
> (Pacific Waterfowl Flyway Council, 1978)

A 21-year banding program of a subpopulation of Pacific
brant conducted by Dr. T. W. Barry with the assistance of
the author, provides the data base for closing some of the
survival and recruitment 'gaps' referred to above. However,
due to a peculiarity in the life history of brant, and geese
in general, existing methods for estimating population
parameters are unable to handle this data set. Briefly, the
peculiarity is as follows: Brant generally do not breed
until they are in their third season (Barry, 1967). The one-
and two-year-old birds do not usually spend the summer with
the breeding adults, and are therefore absent from the

population during banding operations. The goal of this thesis will be to develop an analysis technique applicable to this particular situation by extending the methods and ideas of other researchers in this field. I will then use these procedures to investigate the specific subpopulation of brant referred to above.

I will now discuss the historical development of methods for analyzing banding returns, and capture-recapture analysis in general, to obtain estimates of various population parameters.

Most developments in capture-recapture analysis occurred over the past four decades. The methods dating from 1930 to 1950, and even into the next two decades, are quite simple in concept and were designed primarily to estimate the size of a population, a useful statistic with which to document the status changes of a population. Recently, the scope of these analysis procedures has expanded to include the estimation of survival and recruitment rates, parameters which further the resource manager's understanding of population fluctuations.

For the last forty years two major approaches have been explored, with varying success, for describing population characteristics, the deterministic, and the probabilistic (stochastic) analysis of capture-recapture data (Seber, 1973; Schemnitz, 1980). The first method involves constructing a deterministic life table as is done in human demography. A cohort of individuals of the same age, usually

young, is selected from the population and the number of these surviving to each age is recorded as this group 'moves' through the different age classes. With these data other population characteristics for each age class, such as the mortality rate or the mean expectation of life, may be estimated. This deterministic method, however, is unrealistic, ignoring the stochastic fluctuations in populations and the variability of samples.

Stochastic analysis, on the other hand, deals directly with these features by assigning probabilities to the movements between the age classes. This approach has proven to be extremly flexible and has undergone a great deal of evolution, resulting in some quite useful, although very data-hungry, techniques.

Stochastic methods of parameter estimation are based on information collected by means of some variation or refinement of the basic capture-recapture method employed by Lincoln in 1930 to estimate the total number of North American ducks, N (Seber, 1973). His procedure involved selecting a sample of size n from the population, marking them in a suitable fashion, and then releasing them back into the population. With presumably sufficient time allowed for these marked birds to thoroughly mix with the unmarked, a second sample of size s is drawn by hunters and the number of marked individuals, m, in that collection noted. He reasoned that the proportion of the banded birds that were shot, and their bands returned, would be approximately the

same as the proportion of all of the harvested ducks taken
from the total population. Thus, symbolically, $(m/n) \doteq$
(s/N). This equality provides the simple population estimate
$\hat{N} = s \times (n/m)$, referred to as the Peterson Estimate or
Lincoln Index, the form of which appears throughout much of
the later literature (Seber, 1973).

A simple extension of Lincoln's capture-recapture
scheme was devised by Schnabel in 1938 (Seber, 1973). He
allows the sampling to be repeated periodically (for
example, yearly) for an indefinite time and requires that in
each sample any unmarked individuals captured be tagged and
the number recaptured, of those previously marked, noted.
All of the sampled individuals are then released. With both
Lincoln's and Schnabel's sampling plans an estimate of the
population size only is available. Furthermore, only if the
population is closed, that is, if death and immigration do
not occur, or, if the time between samples is instantaneous
with respect to these features, will these estimates of
Lincoln and Schnabel be valid. The occurrence of death and
immigration alters the proportion of marked individuals in
the population, causing an apparent decrease or an apparent
increase in the estimate of the population size, depending
on whether there is a respective increase or decrease in the
marked proportion. Obviously, this closure requirement
severely limits the usefulness of early attempts at
stochastic estimation for the same reason that life table
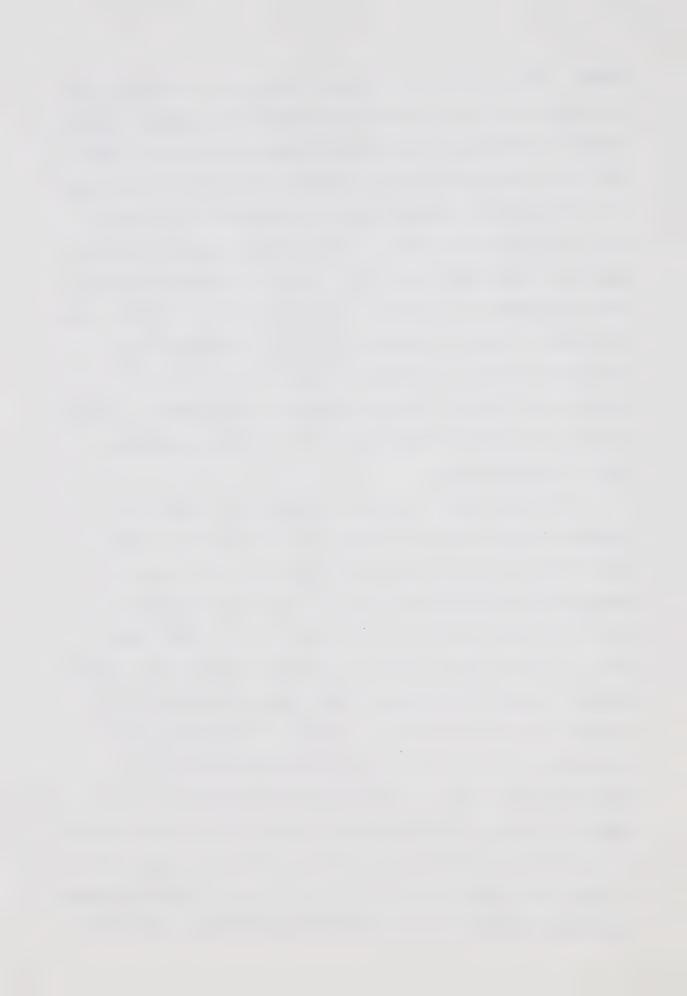methods did not work: population levels tend to fluctuate

over time.

Darroch (1959) first broke through the limitations of assuming a closed population when he developed procedures to account for the possibility of either death or immigration, though not both. He refined Schnabel's long-term census by requiring that each captured individual be marked with a unique number. Since the complete capture history of any individual could now be determined, and hence so could the proportion of individuals which were last captured one, two, three and so on, years ago be determined, the probability of an individual surviving from one sampling period to the next could be introduced to the analysis. Darroch showed that, with the information retrieved from the recaptured animals, estimates of such population parameters as size, survival probability, and the probability of capture can be derived by maximum likelihood techniques.

In 1962 Seber extended Darroch's earlier work by estimating parameters of a population affected by both death and immigration at the same time (Seber, 1962). One major difference, however, existed between Darroch's and Seber's methods. Darroch collected his information from *recaptured* individuals that were returned to the population alive and could thus be recaptured at any time in the future. Seber, on the other hand, used data obtained from animals *recovered* by some process which removed them permanently from the population (e.g. hunting), thus limiting the amount of potential information available from each marked individual

(Seber, 1962; 1970; 1971). Seber's analysis, however, laid the ground-work for further development of a special case of parameter estimation by capture-recapture analysis, that in which the individuals are recovered only once. A large body of literature has accumulated for methods of this type, which are extremely useful in the study of heavily hunted species of waterfowl and fish. The most comprehensive and complete summary is the work by Brownie et al. (1978), which describes in detail fourteen different procedures for analyzing recovery information based on a variety of assumptions. Because these methods were designed for hunted species, they are not applicable to the more endangered or less utilized animals.

Jolly and Seber, working independently, applied Darroch's now standard Schnabel type census to an open population, deriving a general probability distribution designed to work with most single populations which are not split into isolated sub-populations (Jolly, 1965; Seber, 1965). They were the first to organize analysis as a concise method of achieving maximum likelihood estimates so as to account for the possibility of death, recruitment and immigration of new arrivals into the population, and permanent emigration all occuring simultaneously. If the sample is taken from a homogeneous population, one in which all individuals behave in a similar manner, or equivalently, all have the same probability of surviving, then the maximum likelihood estimates of survival probabilities, population

size, number of recruits, *et cetera*, have very simple forms with obvious intuitive interpretations. Known as the Jolly-Seber method, this method of capture-recapture analysis was the basis of the more sophisticated techniques of estimation to be developed later.

Because most species do not form a homogeneous population and are, in fact, composed of many different age groups, for example, young, subadult, and adult, it was necessary to make the Jolly-Seber method more realistic and flexible by allowing for different survival rates among the various age classes, in other words to create a stochastic analogue approximating the rigid deterministic techniques mentioned earlier. To this end Stokes (1980) relaxed the Jolly-Seber assumption of an homogeneous population while using their method to investigate a population of American Woodcocks (*Philohela minor*), a species consisting of two recognizable age classes, young and adult. The young birds of this species mature to breeding adults in one year, a fact Stokes accounted for by assigning different survival probabilities to the two age groups. Her methods were recently generalized to a population consisting of an arbitrary number of one year age classes (Pollock, in press). As with all of these models, Pollock's generalization provides intuitively appealing maximum likelihood estimates for the population parameters.

This then describes advancements in capture-recapture analysis to the point where my analysis begins. The
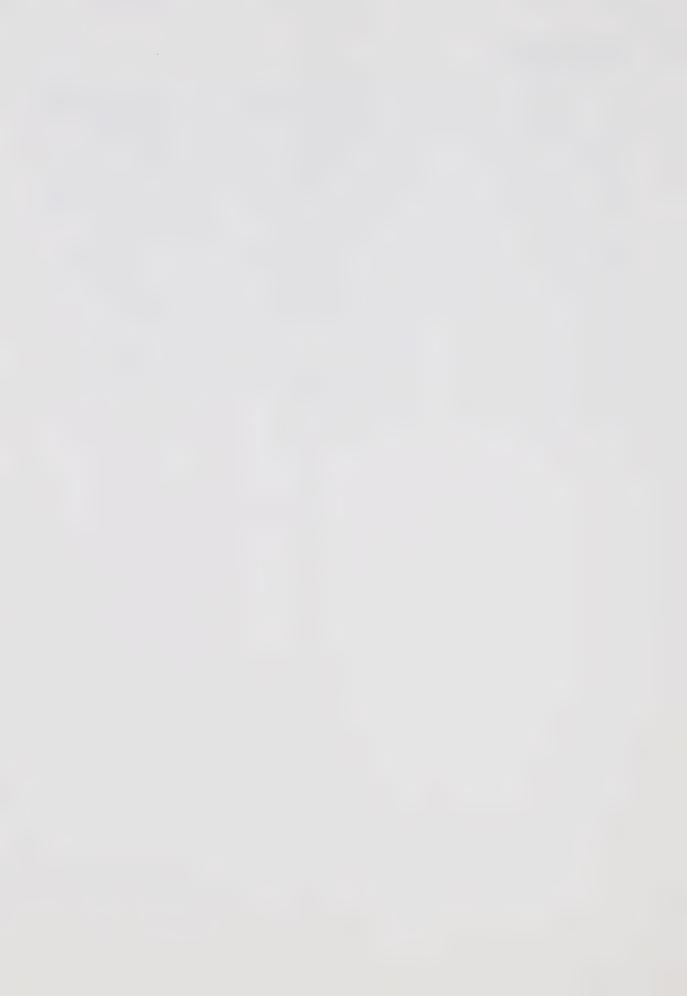
difference between Pollock's general analysis and my problem is this: here I deal with a situation in which the cohort of young do not return to the nesting grounds until they are adult breeding birds. The situation is unique and therefore presents special problems to the statistician.

Acknowledgments

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I. Model

A. Description of Model

As already mentioned, Pollock's method for parameter
estimation in a general age group population is not
applicable to the Pacific brant population which I will be
examining. His method allows *each* one year age group in the
population to have their *own yearly* survival rate while the
Pacific brant require *one* survival rate to cover the *three*
years prior to maturity, and a *yearly* rate thereafter. To
amend this deficiency I will derive estimates for a general
population which is composed of only two discernible age
classes: young and adult. Members of this population follow
the simple life history pattern in which the young become
full breeding adults after a period of 'r' years or seasons
as subadults, and then maintain that adult status until
death. For the duration of this maturing phase, during each
breeding season, most of these non-breeding subadults will
congregate in areas physically separated from the breeding
portion of the population. Those that do not seperate are
not easily captured during sampling because non-breeding
brant have finished molting and are flying before banding
operations take place. Most mature adults return annually to
the breeding grounds. The following model is based on the
procedure for data collection discussed by Seber (1973) in
which samples of the population are taken periodically. Each
unmarked individual captured is marked with a uniquely

numbered band. The number of each recaptured band is
recorded. At the time of any sample the population is
divided among four classes of individuals: young, unmarked
adults, adults which were originally banded as adults, and
finally, those adults originally banded as young. As the
banded young mature they enter the latter class of adults,
while the unbanded young and the adults recruited from
outside the population feed the group of unmarked adults.
Further, as the unmarked adults are captured and banded they
move into the group of adults originally marked as adults.
This describes the general dynamics between the unmarked and
marked portions of the population. With this type of
sampling the capture history, or the times of recapture, of
any individual is established completely, a feature allowing
the much finer movements of banded individuals to be traced.
The treatment of these finer movements is as follows. The
two types of marked adults, those banded-as-adults and those
banded-as-young, are further grouped according to their
capture histories, one group corresponding to each possible
history. The unbanded adults form the group with no capture
history. At each sampling stage, depending on whether they
are captured or not, the members of each capture-history
group can be shunted from one group to another. This
analysis functions by documenting these exchanges
probabilistically.

Assumptions

The following assumptions, typical of those originally made by Jolly and Seber and used in later extensions of their method, appear to be necessary for this type of analysis to be tractable. I have modified and added to them so that they fit the particular situation that I am considering.

1. Every animal in the population, whether marked or unmarked, behaves independently of the others and has the same probability of being captured in the i'th sample. This probability is conditional on the individual being alive and present in the population when the (i+1)'th sample is taken.

2. Every adult has the same probability of surviving from the i'th to the (i+1)'th sample and of being in the population at the time of the (i+1)'th sample, given that it was alive and present in the population immediately after the i'th sample is released.

3. Every young individual has the same probability of surviving from the i'th release to the (i+r)'th sample and of being in the population at the time of the (i+r)'th sample given that it was alive immediately after the i'th sample. 'r' is defined below.

4. No deaths occur as a result of the sampling process.

5. Marked animals do not lose their tags.

Notation

The following symbols will be used to describe the various capture-history groups discussed earlier. The

maximum likelihood estimate of a parameter is denoted with a 'hat' ($\wedge$) over its symbol.

i: Time at which the i'th sample is taken for
            i=1, . . . ,l, where l is the total number of
            samples taken. i is used to identify each
            sample.

$N(i)$:   The total number of individuals in the
            population at time i.

$N(i,y)$:   The number of young in the population at time i.

$N(i,o)$:   The number of unmarked adults in the
            population at time i.

$N(i,j,w)$: The number of individuals (adults), first marked
            as adults, that are in the population at time i,
            who were last captured at time j<i, and have a
            capture history w (w is defined below).

$N(i,j,y,w)$: The number of individuals (adults), first marked
            as young, that are in the population at time i,
            who were last captured at time j<i, and have a
            capture history w.

$S(i)$:   The total number of individuals captured in the
            i'th sample.

$S(i,y)$:   The number of young captured in the i'th sample.

$S(i,o)$:   The number of unmarked adults captured in the
            i'th sample.

$S(i,j,w)$: Those of the $N(i,j,w)$ that are captured in the
            i'th sample.

$S(i,j,y,w)$: Those of the $N(i,j,y,w)$ that are captured in the i'th sample.

w: This is the capture history vector of length $(i-1)$, associated with the $N(i,j,w)$, $N(i,j,y,w)$, $S(i,j,w)$, and $S(i,j,y,w)$.

'w' will consist of $(i-1)$ elements, where the k'th entry will be a '1' if if the individual is captured at time k or a '0' if not captured at time k. A general capture history w, associated with $N(i,j,w)$ say, will then look like:

$w = (...0's or 1's ... ,1,0,...,0)$ The right most '1', in the above expression, represents the time of last capture, j.

The specific capture histories used in this analysis are:

v: $(w;0)$, the capture history of length i with w as the first $(i-1)$ elements and 0 as the last.

s: $(w;1)$

t: $(0,0, ... ,0,1,0,...,0)$; $((r-1)$ zero's$)$

q: $(0,0, ... ,0,1)$

t': $(t;*)$, where $*$ is a string of zeros of appropiate length. This is notation and means that at some previous time an individual had a capture history of t, and has not been captured since.

B(i):   The number of recruits joining the population as unmarked adults between the i'th and the $(i+1)$'th sample.

P(i):   The probability that any individual is captured in the i'th sample.

r: The length of time required for the young of the population to mature and become breeding adults. r is fixed at this value for the duration of the sampling program.

Y(i):   The probability that a young survives from time i to time (i+r).

A(i):   The probability that an adult survives from time i to time (i+1).

M(i):   The number of marked individuals in the population at time i.

Sm(i):   The number of marked individuals captured in the i'th sample.

$$Z(i) = \sum_{j=1}^{i-1} \sum_{h=i+1}^{\ell} (S_{hj} + S_{hjy}) - \sum_{m=i+1}^{i+r-1} \sum_{h=m}^{\ell} S_{hm-r,y,z'}$$

This is the number of adults who were captured in some sample prior to the i'th one, not captured in the i'th sample, but captured subsequently. This expression excludes those individuals which were subadults at time i, and thus were not available for capture at time i.

$$R(i) = \sum_{h=i+1}^{\ell} \left(S_{hi} + S_{hiy}\right) - \sum_{h=i+r}^{\ell} S_{hiy\ell'}$$

R(i) is the number of individuals released from the i'th sample which are subsequently recaptured. Excluded are those which were banded as young in the i'th sample. As with Z(i), these are not available for capture at time i.

B. Development of Model

Conditional Probability Distributions

The following obvious relations describe the division of the population into the four classes, young, unmarked adults, and the two groups of marked adults, according to their banding status.

(1)   N(i) = N(i,y) + N(i,o) +

$$\sum_{j=1}^{i-1} \sum_{w} N(i,j,w) + \sum_{j=1}^{i-1} \sum_{w} N(i,j,y,w)$$

= N(i,y) + N(i,o) + M(i)

(2)   S(i) = S(i,y) + S(i,o) +

$$\sum_{j=1}^{i-1} \sum_{w} S(i,j,w) + \sum_{j=1}^{i-1} \sum_{w} S(i,j,y,w)$$

$$= S(i,y) + S(i,o) + Sm(i)$$

Recalling that a much finer partitioning of the population exists, due to the availability of the capture history, I will now symbolically describe the probabilistic movements between these partitions. My goal is to formulate a joint probability distribution of the numbers of individuals in each of the mark-status classes. To do this I will combine conditional multinomial distributions, using the multiplication rule, to form the joint probability distribution. To save space and to avoid some notational difficulties in the discussion of the probability distributions, I shall write $P(X=x)$ as $P(X)$, not distinguishing between a random variable and one of its possible values.

Consider first the conditional distribution of the number of young caught in the i'th sample, $S(i,y)$, given the number of young in the population, $N(i,y)$, and the probability of being captured, $P(i)$. There are two possible fates confronting a member of $N(i,y)$. He may escape capture at time i or be captured, becoming a member of the $S(i,y)$. Following the assumptions, the distribution of $S(i,y)$ is:

$$(3) \qquad P(S_{iy} \mid N_{iy}, P_i) = \binom{N_{iy}}{S_{iy}} P_i^{S_{iy}} (1 - P_i)^{N_{iy} - S_{iy}}$$

Secondly, the distribution of the unmarked adults in the population at time $(i+1)$, $N(i+1,o)$, and in the i'th sample, $S(i,o)$, is also conditional on several quantities. These are the number of unmarked adults present at time i, $N(i,o)$, the number of unmarked recruits entering the population between time i and $(i+1)$, $B(i)$, the probability of capture, $P(i)$, and the probability of surviving to time $(i+1)$, $A(i)$. The distribution is found, as before, by documenting the possible fates facing the $N(i,o)$.

A member of $N(i,o)$ may have one of three things occur to it between time i and $(i+1)$.

1) He can be captured in the i'th sample and hence become a member of the $S(i,o)$ and be marked. After release he will next appear, if at all, as a member of $N(k,i,w)$ for some $k>i$.

2) He may not be captured and thereby become a member of $N(i+1,o)$. This class has, however been diluted by the $B(i)$ unmarked adults joining the population as recruits between time i and $(i+1)$.

3) He may not be captured and then leave the population by dying or permanently emigrating.

These three mutually exclusive possibilities give rise to the following multinomial distribution expression:

$$(4)\quad P\left(S_{io}, N_{i+1o} \mid N_{io}, B_i, P_i, A_i\right) = \binom{N_{io}}{S_{io}} P_i^{S_{io}} (1-P_i)^{N_{io}-S_{io}} \times$$

$$\binom{N_{io}-S_{io}}{N_{i+1o}-B_i} A_i^{N_{i+1o}-B_i} (1-A_i)^{N_{io}-S_{io}-N_{i+1o}+B_i}$$

Similarly between times i and (i+1), members of N(i,j,w). have three mutually exclusive fates to choose from.

1) Being captured and becoming a member of S(i,j,w). After release he will next appear, if at all, as a member of N(k,i,w) for some k>i.

2) Not being captured and surviving to time (i+1), that is becoming a member of N(i+1,j,v).

3) Not being captured and then dying or permanently emigrating from the population.

Thus the distribution of S(i,j,w), and N(i+1,j,v) given N(i,j,w), P(i) and A(i) is:

$$(5)\quad P\left(S_{ij\omega}, N_{i+1jv} \mid N_{ij\omega}, P_i, A_i\right) = \binom{N_{ij\omega}}{S_{ij\omega}} P_i^{S_{ij\omega}} (1-P_i)^{N_{ij\omega}-S_{ij\omega}} \times$$

$$\binom{N_{ij\omega}-S_{ij\omega}}{N_{i+1jv}} A_i^{N_{i+1jv}} (1-A_i)^{N_{ij\omega}-S_{ij\omega}-N_{i+1jv}}$$

A similar distribution is formed for the S(i,j,y,w) and N(i+1,j,y,v), the adults first marked as young:

$$(6) \quad P(S_{ijy\omega}, N_{i+1jy\nu} | N_{ijy\omega}, P_i, A_i) = \binom{N_{ijy\omega}}{S_{ijy\omega}} P_i^{S_{ijy\omega}} (1-P_i)^{N_{ijy\omega} - S_{ijy\omega}} X$$

$$\binom{N_{ijy\omega} - S_{ijy\omega}}{N_{i+1jy\nu}} A_i^{N_{i+1jy\nu}} (1-A_i)^{N_{ijy\omega} - S_{ijy\omega} - N_{i+1jy\nu}}$$

Each member of the sample (S(i,y), S(i,o). S(i,j,w),
or S(i,j,y,w)) also has several fates. He can either
survive after release, becoming a member of N(i+r,i,y,t),
N(i+1,i,q), N(i+1,i,s) or N(i+1,i,y,s) respectively, or he
may leave the population by dying or permanently emigrating.
The distribution then of N(i+r,i,y,t). N(i+1,i,q) N(i+1,i.s)
and N(i+1,i,y,s) given the quantities S(i,y), S(i,o),
S(i,j,w), S(i,j,y,w), A(i) and Y(i) is:

(7) $P\left(N_{i+riyt}, N_{i+iiq}, N_{i+iis}, N_{i+iys} \mid S_{iy}, S_{io}, S_{ijw}, S_{ijyw}, Y_i, A_i\right) =$

$$\binom{S_{iy}}{N_{i+riyt}} Y_i^{N_{i+riyt}} (1 - Y_i)^{S_{iy} - N_{i+riyt}}$$

$$\times \binom{S_{io}}{N_{i+iiq}} A_i^{N_{i+iiq}} (1 - A_i)^{S_{io} - N_{i+iiq}}$$

$$\times \binom{S_{ijw}}{N_{i+iis}} A_i^{N_{i+iis}} (1 - A_i)^{S_{ijw} - N_{i+iis}}$$

$$\times \binom{S_{ijyw}}{N_{i+iiys}} A_i^{N_{i+iiys}} (1 - A_i)^{S_{ijyw} - N_{i+iiys}}$$

Joint Probability Distribution Function

The joint probability distribution for all of the possible options open to the members of the population, taken over all of the samples, is formed by the product of the conditional multinomial distributions (3) through (7) above. This product is taken over all possible capture histories, w, over all j (0<j<i) and over all i, (0<i<(l+1)). Using relations (1) and (2) to simplify expressions, the joint distribution becomes:

(8)

$$
\prod_{\substack{0<j<i \\ 0<i<l}} P\left[\begin{array}{l} S_{iy}, S_{io}, S_{ijw}, S_{ijyw}, N_{i+1o}, N_{i+1jv}, \\ N_{i+1jyv}, N_{i+1iyt}, N_{i+1i8}, N_{i+1i5}, N_{i+1iys} \end{array} \middle| N_i, B_i, P_i, Y_i, A_i \right] =
$$

$$
\prod_{i=1}^{l} \prod_{j=1}^{i-1} \prod_{w} \left\{
\begin{array}{l}
P_i^{S_i} (1-P_i)^{N_i - S_i} \times Y_i^{N_{i+1iyt}} (1-Y_i)^{S_{iy} - N_{i+1iyt}} \\[2em]
\times A_i^{\left[N_{i+1} - N_{i+1y} - N_{i+1i+1-ryt} - B_i\right]} \\[2em]
\times (1-A_i)^{\left[N_i - N_{iy} - N_{i+1} + N_{i+1y} + N_{i+1i+1-ryt} + B_i\right]}
\end{array}
\right\}
$$

$$
\times \left[K_1 \times K_2 \times K_3 \times K_4\right] \qquad \text{where,}
$$

$$K_1 = \frac{N_{io}!}{(N_{i+1o} - B_i)! \; (N_{io} - S_{io} - N_{i+1o} + B_i)! \; (S_{io} - N_{i+1iz})! \; N_{i+1iz}!}$$

$$K_2 = \frac{N_{iy}!}{(N_{iy} - S_{iy})! \; (S_{iy} - N_{i+riyt})! \; N_{i+riyt}!}$$

$$K_3 = \frac{N_{ij\omega}!}{(N_{ij\omega} - S_{ij\omega} - N_{i+1jv})! \; N_{i+1jv}! \; (S_{ij\omega} - N_{i+1is})! \; N_{i+1is}!}$$

$$K_4 = \frac{N_{ijy\omega}!}{N_{i+1jyv}! \; (N_{ijy\omega} - S_{ijy\omega} - N_{i+1jyv})! \; (S_{ijy\omega} - N_{i+1iys})! \; N_{i+1iys}!}$$

C. Estimation Equations

To justify the estimation procedures used in this section I will briefly discuss Jolly's (1965) approach to this problem, an approach which I have adapted to this thesis. Strictly speaking, the population quantities $N(i+1,o)$, $N(i+1,j,v)$ and $N(i+1,j,y,v)$ are random variables, affected by the random numbers of individuals surviving over time intervals prior to time $(i+1)$, and are not fixed characteristics (parameters) of the population. As such the probability distribution (8) is not a true likelihood since it is not just the probability of obtaining the observations $S(i,o)$, $S(i,j,w)$, $S(i,j,y,w)$, and $S(i,y)$, but of obtaining both these observations and the $N(i+1,o)$, $N(i+1,j,v)$ and $N(i+1,j,y,v)$ given the parameters $N(1)$, $B(i)$, $P(i)$, $A(i)$ and $Y(i)$. Jolly (1965) reasons that (8) can reasonably be regarded as a likelihood function if population variables at time i are being estimated since in this case the $N(i,o)$, $N(i,j,w)$ and $N(i,j,y,w)$ will be parameters of a distribution conditional on events up to time i, and so do not have a random component. However, when variables prior to time i are being estimated, Jolly (1965) claims that intuitively to treat these variables as parameters throughout will lead to estimates that are close to the true maximum likelihood estimates. Following Jolly's justification, I will proceed by considering (8) as a true likelihood function L, of a set of population parameters. When deriving the estimate of a parameter, say U, it is easier to follow the subsequent

derivations if the likelihood function (8) is written as the product of two functions one containing all of those terms of (8) which are independent of U (call it K) and the other containing all those terms dependent on U, F(U) say. Thus, L(U) = K x F(U). The motivation for this will become clear shortly.

The maximum likelihood estimates of the three probabilities, P(k), A(k) and Y(k) are found by differentiating the natural logarithm of (8) with respect to each of them and equating the result to zero. Since the probability distribution function is concave upwards (and hence its logarithm is concave downwards), the solution of this equation will locate the maximum of each parameter. Thus considering (8) as a function of P(k) (the probability of capture):

$$\ln\left[L(P_k)\right] = \ln(K) + S_k \ln(P_k) + (N_k - S_k)\ln(1 - P_k),$$

$$\text{for } k = 1, \cdots, l.$$

and so:

$$\frac{\partial \ln L(P_k)}{\partial P_k} = \frac{S_k}{P_k} - \frac{(N_k - S_k)}{(1 - P_k)}$$

Setting this derivative to zero results in the following estimate of the probability of capture:

(9) $\quad \hat{P}_k = \dfrac{S_k}{\hat{N}_k}$, $\quad$ for $k = 1, \cdots, \ell$.

Similarly the logarithm of the likelihood of the probability that the young survive to time (k+r) is:

$$\ln L(Y_k) = \ln(K) + N_{k+r\,ky\pm} \ln(Y_k) - (S_{ky} - N_{k+r\,ky\pm}) \ln(1 - Y_k) ,$$

for $k = 1, \cdots, (\ell - r)$.

and

$$\frac{\partial \ln L(Y_k)}{\partial Y_k} = \frac{N_{k+r\,ky\pm}}{Y_k} - \frac{(S_{ky} - N_{k+r\,ky\pm})}{(1 - Y_k)}$$

from which the survival rate is estimated by:

(10) $\quad \hat{Y}_k = \dfrac{\hat{N}_{k+r\,ky\pm}}{S_{ky}}$, $\quad$ for $k = 1, \cdots, (\ell - r)$.

Intuitively, (10) uses as its estimate the proportion of those animals initially marked as young at time k who have managed to survive to become adults at time (k+r).

For the adult survival rate, A(k), the likelihood function is:

$$\ln L(A_k) = \ln(K) + \left[N_{k+1} - N_{k+1 y} - N_{k+1\, k+1-ryt} \right] \ln(A_k) +$$

$$\left[N_k - N_{ky} - N_{k+1} + N_{k+1 y} + N_{k+1\, k+1-ryt} + B_k \right] \ln(1 - A_k)$$

for $k = 1, \ldots, (\ell-1)$.

and:

$$\frac{\partial \ln L(A_k)}{\partial A_k} = \frac{N_{k+1} - N_{ky} - N_{k+1\, k+1-ryt}}{A_k} -$$

$$\frac{N_k - N_{ky} - N_{k+1} + N_{k+1 y} + N_{k+1\, k+1-ryt} + B_k}{(1 - A_k)}.$$

Set this to zero and solve for the estimate of A(k).

$$(11) \quad \hat{A}_k = \frac{\hat{N}_{k+1} - \hat{N}_{k+1 y} - \hat{N}_{k+1\, k+1-ryt} - \hat{B}_k}{\hat{N}_k - \hat{N}_{ky}},$$

for $k = 1, \ldots, (\ell-1)$.

Intuitively the denominator of (11) is the number of adults, whether marked or unmarked, in the population at time k. The numerator is the number of adults at time (k+1), after removing the young of the year and any adults which could not possibly be present at time k but were at time (k+1). The quotient then is the proportion of adults which have

survived to time (k+1).

The remaining maximum likelihood estimates (for integer-valued quantities) are found by equating the first backwards difference of the logarithm of the likelihood function to zero. That is, for some parameter G,

if $\qquad$ $L(G) = K \times F(G)$

then $\qquad$ $\ln(L(G)) = \ln(K) + \ln(F(G))$

and $\qquad$ $\Delta \ln(L(G)) = \ln(L(G)) - \ln(L(G-1))$

$\qquad\qquad\qquad = \ln(F(G)) - \ln(F(G-1))$,

which is independent of K.

The maximum likelihood estimate then of G is the greatest integer less than or equal to 'g' such that $\Delta \ln(L(g)) = 0$, that is: $\ln(F(g)) = \ln(F(g-1))$. For this application though I will consider the maximum likelihood estimate to be the solution of

$\Delta \ln(L(g)) = 0$.

From the above discussion the number of recruits B(k) will be estimated as follows. From (8):

$$L(B_k) = \frac{K \; A_k^{-B_k} \; (1 - A_k)^{B_k}}{(N_{k+1 \, 0} - B_k)! \; (N_{k0} - S_{k0} - N_{k+1 0} + B_k)!} \; ,$$

$for \; k = r, \ldots, (\ell - r - 1)$

Then $\Delta \ln L(B_k) = \ln L(B_k) - \ln L(B_k - 1)$

$$= \ln(1 - A_k) - \ln(A_k) + \ln(N_{k+1\,0} - B_k + 1) -$$

$$\ln(N_{k0} - S_{k0} - N_{k+1\,0} + B_k)$$

and equating this to zero gives:

$$\hat{B}_k = \hat{N}_{k+1\,0} - \hat{A}_k \left[1 + \hat{N}_{k0} - S_{k0}\right] + 1$$

which reduces to

$$(12) \quad \hat{B}_k = \hat{N}_{k+1\,0} - \hat{A}_k \left(N_{k0} - S_{k0}\right),$$

for $k = r, \ldots, (\ell - r - 1)$

since the relative error in equating N(k+1,o) - B(k) + 1 to
N(k+1,o) - B(k) for large N(k+1,o) is negligible. This
estimate for B(k) is the estimated number of unmarked adults
at time (k+1), with all of those unmarked adults which had
survived from time k removed. This leaves an estimate of
only those adults recruited into the population between
times k and (k+1). The more complex derivations that remain
constitute the Appendix.

To round out the discussion of the model, I will give
the final forms of the estimation equations and provide an
intuitive discussion of each.

First, the number of marked adults present in the population at some time k is estimated by the following equation:

$$(13) \qquad \hat{M}_k = \frac{Z_k}{R_k} \left(S_{k0} + S_{mk} \right) + S_{mk} ,$$

for $k = r, \dots, (\ell-r)$.

An intuitive explanation of this equation is as follows. To estimate the number of marked individuals in the population at time k, M(k), it is necessary to augment the number of these actually seen, Sm(k), by an estimate of the number that were present but not seen. There were Z(k) marked animals present in the population at the time, but not seen then. However, they are seen at some time in the future. This quantity is increased by multiplying it by the ratio of the number of marked animals known to exist just after the k'th sampling (S(k,o) + Sm(k)) to the number of these that are subsequently recaptured, R(k). If the proportion of individuals subsequently recaptured is roughly the same for both classes, then $Z(k) \left[S(k,o) + Sm(k) \right] / R(k)$ estimates the number of marked individuals present at time k but not captured then. By adding this term to Sm(k), one obtains the maximum likelihood estimate of M(k). This equation for M(k) is the key to the whole estimation problem since it is involved in most of the remaining estimation equations.

The equation for estimating the current size of the population takes the form of the simple Peterson estimate employed by Lincoln in 1930 (Seber, 1973):

$$(14) \quad \hat{N}_k = \hat{M}_k \frac{S_k}{S_{mk}} \quad ,$$

for $k = r, \ldots, (\ell-r)$.

Here, the number of individuals in the i'th sample, S(k), is inflated by the proportion of marked adults in the population which are captured in that sample.

The probability of capture is simply estimated by proportion of the population which were unable to evade capture at that time:

$$(15) \quad \hat{P}_k = \frac{S_k}{\hat{N}_k} = \frac{S_{mk}}{\hat{M}_k} \quad ,$$

for $k = r, \ldots, (\ell-r)$.

The equation determining the number of young, which survive the 'r' years, to emerge as mature breeding adults at time k is:

$$(16) \quad \hat{N}_{k\,k-ry\pm} = \hat{M}_k \frac{\sum\limits_{h=k}^{\ell} S_{h\,k-ry\pm'}}{S_{mk} + Z_k} \quad ,$$

for $k = (r+1), \ldots, (\ell-r)$.

The denominator of (16) counts all those individuals which were captured in and prior to the k'th sample and were subsequently recaptured. The summation in the numerator tallies the individuals which were in the (k-r)'th sample as young (and are thus 'r' year old adults at time k) and were next seen in some k or later sample. Thus the expression represents the proportion of individuals subsequently recaptured that are 'r' years old at time k. This proportion of the marked animals, $\hat{M}(k)$, provides the desired estimate.

With the result of (16) the probability of the young surviving the 'r' years to adulthood is easily estimated by the proportion of the young marked at time k which are in the population at time (k+r):

$$(17) \quad \hat{Y}_k = \frac{N_{k+r\,kyt}}{S_{ky}} \, ,$$

for $k = 1, \cdots, (\ell - 2r)$.

Similarly the probability of adult survival from time k to (k+1) is the ratio of appropriate marked individuals:

$$(18) \quad \hat{A}_k = \frac{\hat{M}_{k+1} - \hat{N}_{k+1\,k+1-ryt}}{\hat{M}_k + S_{ko}} \, ,$$

for $k = r, \cdots, (\ell - r - 1)$.

This is simply the proportion of marked adults at time (k+1) which have survived from time k. However the young that are just becoming 'r' year old adults at time (k+1) must be

discounted as this cohort was not part of the marked adult class at time k.

The estimates for the number of unmarked adults and the young in the population both employ the Peterson type estimation equation:

$$(19) \quad \hat{N}_{ko} = \frac{S_{ko}}{\hat{P}_k} = \frac{S_{ko}}{S_k} \hat{N}_k$$

for $k = r, \ldots, (\ell-r)$.

$$(20) \quad \hat{N}_{ky} = \frac{S_{ky}}{\hat{P}_k} = \frac{S_{ky}}{S_k} \hat{N}_k$$

for $k = r, \ldots, (\ell-r)$.

Finally, repeating equation (12), the number of recruits (unmarked) to the population from time k to (k+1) is estimated by:

$$(12) \quad \hat{B}_k = \hat{N}_{k+1\,o} - \hat{A}_k (N_{ko} - S_{ko}) ,$$

for $k = r, \ldots, (\ell-r-1)$.

N(k+1,o) is adjusted for the number of unmarked adults already in the population at time (k+1) which have survived to time k. The remaining quantity is the estimated number of

recruits.

Figure 1. Map Showing the Location of the
Anderson River Delta

Figure 2. Map of the Anderson River Delta

II. Data Analysis

A. Background

The brant is a migratory goose, breeding in circumpolar regions and wintering further south along the sea coast. In summer they inhabit loose colonies near salt water wherever suitable habitat is found. I recognize three subspecies of brant in the world, European brant (*B. b. bernicla*), Atlantic brant (*B. b. hrota*), and Pacific brant (*B. b. nigricans*), the latter two occurring in North America (Barry, 1967).

Atlantic brant, found along the eastern seaboard in winter from Massachusetts to South Carolina, move north in the spring to breed in the central and eastern arctic. Pacific brant, on the other hand, winter along the west coast from British Columbia to the Baja California Peninsula. They breed along the arctic coast from western Alaska to the central arctic and the high arctic islands. Because pairing takes place during the southwards migration and on into the winter, and copulation occurs during the northwards migration, there is little interbreeding between Atlantic and Pacific brant where their summer ranges overlap in the central arctic (Barry, 1967; Bellrose, 1976; Palmer, 1976).

The data to be analyzed were obtained from a subpopulation (colony) situated in the Anderson River Delta on the Beaufort Sea coast in the Canadian western arctic

(Fig. 1). This banding program was conducted by Dr. T. W. Barry of the Canadian Wildlife Service, with the assistance of the author.

The Anderson River, emptying into the Beaufort Sea 150 kilometers east of the great Mackenzie River Delta, has formed a rich tidal delta covering about 65 square kilometers of shallow channels and low flat islands (Fig. 2). The brant arrive there in late May. After the snow clears and the ground dries, they begin to establish territories and nest sites on the lower islands of the outer delta. Non breeding brant, yearlings and two-year-olds, do not ordinarily use the delta but spend the summer elsewhere in the arctic. After the·hatch in early July family groups gradually begin to congregate into a number of large flocks scattered throughout the delta and by the end of the month the adults have begun to molt. These flocks usually occupy the traditional molting sites of Kettle Hole Point, Brant Island, Study Area Island, Fox Den Island, Juncus Island, Triangle Island, Loon Channel, Middle Creek, and Shearpin Creek along the brackish tide zone of the outer delta. Within three or four weeks the adults are flying again, somewhat synchronous with the first flight of the young in the early part of August. In late August and early September the brant begin moving westwards along the coast, mingling with other groups as they work their way towards their common staging area in Izembek Bay, Alaska. From there all migrate south to their coastal haunts for the winter

(Bellrose, 1976; Palmer, 1976).

B. Methods

The timing of the annual molt to coincide with the initial flightless period of the young provides an excellent opportunity to capture both the young and adults for banding. The brant's propensity for flocking during the molt somewhat simplifies the logistics of capture but does not make it altogether easy.

Banding drives were undertaken during the last week of July and the first week in August when the young geese were large enough to retain a metal leg band and strong enough to withstand the stress of the banding. Brant were herded into circular banding pens, 10 to 15 meters in diameter, constructed of fine meshed fish net (herring seine) hung from poles 1.5 meters high and staked down to the ground. Two 50 meter long leads funneled the geese into the pen. By hazing about twenty birds at a time into a small catch pen, within the main pen, banding personnel could easily capture and mark the birds with a numbered band placed around the lower right leg. The age class, either young or adult, and sex of each bird banded was recorded with its band number.

When a previously banded bird was encountered in these operations its band number, age class (adult), and sex were recorded. Often the recaptured band was so worn as to be partially or completely illegible; these were removed and replaced, and the new number cross-referenced with the old

one in the records. Most of these illegible bands could be read after being chemically etched, a process that removed the top layers of the metal, exposing the indentations of the numbers beneath the surface.

During the twenty-one years from 1959 to 1979, as many as possible of the nine traditional molting flocks were sampled. There were, however, variations in the methods of herding. Between 1959 and 1973 a small motor boat and several people were used to herd and manoeuvre the brant into the pens. Wind, tide, the many shallow channels and hidden mudbars, combined with the rather stubborn nature of the brant, complicated the process of herding by boat. These factors limited the choice of banding areas sampled to Kettle Hole Point, Middle Creek, Shearpin Creek and Juncus Island. Since 1973 helicopter aircraft have been used to locate the geese, transport people, and to help herd. Within the limitations of funds and time this allowed a greater number of the brant to be sampled, especially from the molting flocks that were previously inaccessible by boat.

In 1968 and again in 1971 no banding operations were attempted. Furthermore, banding was not possible in 1974 when all nesting attempts of brant failed due to predation by foxes (*Alopex lagopus* and *Vulpes vulpes*). As a result of the foxes' activities, the adult brant left the delta area in a molt migration. For these three 'missing years' I have generated data conforming to the general trend of other years. For the purpose of testing my estimation equations,

the real banding data and the generated data will be sufficient. The problem of missing data in capture-recapture experiments is very real, and is open to further exploration.

Over the years several different types of bands were used in an attempt to reduce the loss of bands from salt water corrosion. Until about 1967 soft aluminum bands were in use, which proved to have a very low resistance to corrosion, often becoming completely illegible within two years. In many cases the band was found to be so weakened that it was ready to fall off the leg. Since 1967, but with the exception of 1973 when aluminum was used again, the bands were of harder alloys (monel and nickalloy). These have been more successful.

Each spring at the Anderson Delta from 1959 to 1965 and from 1972 to 1979 a portion of the brant's nesting habitat was searched for nests, the clutch size of each one being recorded. These data are used to estimate the maximum number of young produced by the Anderson River brant and provide a check on the results of the analysis.

C. Results

In the estimation equations from Part I that are used in this section r is given the value of three, the number of years required for the young brant to mature. Tables I, II, and III summarize the raw capture-recapture data collected from 1959 to 1979. The distribution of the recaptured adults

which were originally banded as adults is given in Table I
for each of the banding years according to the time of last
capture. Table II shows the distribution of recaptured
adults originally banded as young. These two tables, in
effect, show the number of sampled individuals in each of
the capture-history groups. Certain row and column sums used
in the estimation equations are given in these tables as
well.

The number of the banded three-year-old adults just
returning to the population is shown in Table III. These
birds may have been more than three years old when they were
finally recaptured, but they were all new mature adults at
the appropiate time. Individuals of this sort which are
recaptured when they are three years old appear along the
upper diagonal, while those birds which are recaptured later
in life appear along a diagonal deeper within the table.

The only other remaining information required for the
parameter estimates is the number of unmarked adults,
$S(k,o)$, and the number of young of the year, $S(k,y)$,
captured in each sample. These data are presented in Table
IV, along with a condensation of the information contained
in Tables I, II and III presented in the form of the sums
which appear directly in the estimation equations. Applying
equations (12) through (20) from the analysis in Part I,
with r set to three, results in the parameter estimates
given in Table V.

In summarizing the more important and useful results, I have deleted the first estimate for each parameter because these were calculated with insufficient data, that is, there were very few capture-recapture occurrences in the first several years of the study. The estimated brant population, $N(k)$, at Anderson River had a mean of 4349 birds per year (including young of the year, and both the marked and unmarked adults), ranging from 2801 to 8134 individuals. The marked adult portion of this population, $M(k)$, generally numbered 814, while the mean number of unmarked adults and young was 1578 and 1957 respectively per year.

The adult brant appear to have a high probability of surviving from year to year (mean $\hat{A}(k) = 0.70$). Their chances of surviving for three years ($\hat{p} = 0.34$) is significantly high as compared to the probability of the young surviving for three years (mean $\hat{Y}(k) = .15$). Unmarked brant were recruited into the population at a mean rate of 808 birds per year.

The clutch-size data collected at Anderson River is summarized in Table VI. The portion of the nesting habitat surveyed each year is used to estimate the maximum number of young that could be produced, generally about 5600. However, the 5600 young is a gross over-estimate of the number of those actually available for banding, since predators take many of the eggs and young long before banding commences. Moreover, the estimate of the percent of habitat covered is rough and serves only as a check on the analysis results.

Table VII shows that from 3% to 33% of the bands of recaptured birds had to be replaced each year, with a total of 230 replacements from 1962 to 1979. Eleven bands (5%) were so corroded by salt water that chemical etching failed to bring out the numbers. The life of the softer aluminum bands which had to be replaced is between three and seven years. Only (3%) of the harder bands used in the later years had to be replaced.

Banding locations varied considerably, the most consistently sampled sites being Kettle Hole Point and Middle Creek. The remaining 7 saw more intermittent use. The distribution of the banding drives made each year is given in Table VIII.

The individual brant at Anderson River have a propensity to nest and molt within the same areas of the delta year after year. To illustrate this phenomenon I have tabled all of the recapture occurrences by location, according to the location of previous capture (Table IX). Many of the nine banding locations are in close proximity to one another so I have recognized four nearly autonomous brood rearing areas within the delta. Examination of this data suggests that intermixing between sites is low, 57% of the capture-recapture occurrences take place in the same areas. Treating Table IX as a four by four contingency table and applying a Chi-Square test for independence indicates that recapture location is very dependent on the site of previous capture (Chi-Square = 737.0, d.f. = 9).

The source for the following tables is the unpublished field notebooks of Dr. T. W. Barry and the author.

Table I: Banding Distribution of S(i,j)

Recapture Year i

Capture

Year j	1960	1961	1962	1963	1964	1965	1966
1959	0	0	0	1	0	0	0
1960	(0)	7	13	8	0	2	0
1961		(7)	2	7	0	0	0
1962			(15)	33	2	9	10
1963				(49)	23	39	17
1964					(25)	21	15
1965						(71)	44
1966							(86)
1967							
1968							
1969							
1970							
1971							
1972							
1973							
1974							
1975							
1976							
1977							
1978							

Table I: Continued

Recapture Year i

Capture Year j	1967	1968	1969	1970	1971	1972	1973
1959	0	0	0	0	0	0	0
1960	0	0	0	0	0	0	0
1961	0	1	0	0	0	0	0
1962	0	0	0	0	0	0	0
1963	4	3	1	2	0	2	2
1964	19	10	5	0	0	1	0
1965	33	18	11	0	15	3	2
1966	69	40	35	27	23	17	4
1967	(125)	53	41	21	23	25	6
1968		(125)	62	23	29	17	11
1969			(155)	39	19	22	14
1970				(112)	15	6	3
1971					(124)	43	26
1972						(136)	71
1973							(139)
1974							
1975							
1976							
1977							
1978							

Table I: Continued

Recapture Year i

Capture Year j	1974	1975	1976	1977	1978	1979	Row Sum
1959	0	0	0	0	0	0	(1)
1960	0	0	0	0	0	0	(30)
1961	0	0	0	0	0	0	(10)
1962	0	0	0	0	0	0	(54)
1963	0	2	0	0	0	0	(95)
1964	0	0	0	0	0	0	(71)
1965	1	0	0	1	0	0	(128)
1966	1	0	3	0	1	0	(220)
1967	3	4	2	1	0	1	(180)
1968	15	5	1	0	1	0	(164)
1969	8	12	2	0	1	0	(117)
1970	2	6	1	0	2	0	(35)
1971	11	4	2	4	1	1	(92)
1972	43	36	16	14	11	7	(198)
1973	96	106	14	4	16	4	(240)
1974	(180)	69	42	15	17	6	(149)
1975		(244)	107	23	81	33	(244)
1976			(190)	27	50	27	(104)
1977				(89)	41	14	(55)
1978					(222)	170	(170)
						(263)	

Table II: Banding Distribution of S(i,j,y)

Recapture Year i

Capture

Year j	1960	1961	1962	1963	1964	1965	1966
1959	0	0	0	0	0	0	0
1960	(0)	0	0	5	1	1	0
1961		(0)	0	0	0	0	0
1962			(0)	0	0	2	0
1963				(5)	0	0	2
1964					(1)	0	0
1965						(3)	1
1966							(3)
1967							
1968							
1969							
1970							
1971							
1972							
1973							
1974							
1975							
1976							
1977							
1978							

Table II: Continued

Recapture Year i

Capture

Year j	1967	1968	1969	1970	1971	1972	1973
1959	0	0	0	0	0	0	0
1960	0	0	0	0	0	0	0
1961	0	0	0	0	0	0	0
1962	2	2	1	0	0	0	0
1963	3	2	0	0	0	3	1
1964	5	3	2	1	1	0	0
1965	0	1	2	1	0	3	0
1966	0	0	0	0	4	1	2
1967	(10)	1	0	1	11	14	11
1968		(9)	0	0	3	7	9
1969			(5)	0	0	3	3
1970				(3)	0	0	2
1971					(19)	0	0
1972						(31)	5
1973							(33)
1974							
1975							
1976							
1977							
1978							

Table II: Continued

Recapture Year i

Capture Year j	1974	1975	1976	1977	1978	1979	Row Sum
1959	0	0	0	0	0	0	(0)
1960	0	0	0	0	0	0	(7)
1961	0	0	0	0	0	0	(0)
1962	0	0	0	0	0	0	(7)
1963	0	0	0	0	0	0	(11)
1964	1	0	0	0	0	0	(13)
1965	0	0	0	0	0	0	(8)
1966	2	1	0	0	0	0	(10)
1967	7	5	2	1	3	2	(58)
1968	6	4	1	0	2	1	(33)
1969	7	6	0	0	2	0	(21)
1970	1	0	0	1	1	0	(5)
1971	4	4	2	1	0	1	(12)
1972	0	14	9	7	6	3	(44)
1973	0	13	9	2	9	2	(35)
1974	(28)	0	5	9	8	3	(25)
1975		(47)	3	2	22	18	(45)
1976			(31)	3	8	13	(24)
1977				(26)	3	5	(8)
1978					(64)	20	(20)
						(68)	

Table III: Banding Distribution of $S(i, i-m, y, t')$

Year Originally Banded as Young, (i-3)

Re-Capture Year i	1959	1960	1961	1962	1963	1964
1962	0	1960				
1963	0	5	1961			
1964	0	1	0	1962		
1965	0	1	0	2	1963	
1966	0	0	0	0	2	1964
1967	0	0	0	2	3	5
1968	0	0	0	1	2	4
1969	0	0	0	0	2	3
1970	0	0	0	0	0	1
1971	0	0	0	0	0	2
1972	0	0	0	0	3	0
1973	0	0	0	0	1	0
1974	0	0	0	0	0	0
1975	0	0	0	0	0	0
1976	0	0	0	0	0	0
1977	0	0	0	0	0	0
1978	0	0	0	0	0	0
1979	0	0	0	0	0	0
Sum	(0)	(7)	(0)	(5)	(13)	(15)

Table III: Continued

Year Originally Banded as Young, (i-3)

Re-Capture Year i	1965	1966	1967	1968	1969	1970
1968	5					
1969	7	6				
1970	2	1	8			
1971	0	4	8	10		
1972	3	1	14	9	3	
1973	0	2	11	3	3	2
1974	0	0	0	5	0	3
1975	0	1	5	0	6	0
1976	0	0	2	1	0	0
1977	0	0	1	1	0	1
1978	0	0	3	0	2	1
1979	0	0	2	2	0	0
Sum	(17)	(15)	(54)	(31)	(14)	(7)

Table III: Continued

Year Originally Banded as Young, (i-3)

Re-Capture Year i	1971	1972	1973	1974	1975	1976
1974	13					
1975	11	14				
1976	3	6	5			
1977	2	5	1	9		
1978	4	5	7	12	18	
1979	2	3	2	9	14	9
Sum	(35)	(33)	(15)	(30)	(32)	(9)

Table IV: Summary of Banding Results

Banding Year

Sample Observ.	1959	1960	1961	1962	1963	1964	1965
S(k,o)	12	105	19	264	471	158	525
S(k,y)	17	246	52	334	447	170	491
Sm(k)	0	0	7	15	54	26	74
S(k)	29	351	78	613	972	354	1090
*		1	31	26	33	113	123
**			7	7	5	18	28
***				0	7	0	5
****	1	37	10	61	106	84	136
Z(k)			24	19	18	95	95
R(k)	1	30	10	56	93	69	119

$$* \; \sum_{j=1}^{k-1} \sum_{h=k+1}^{\ell} \Big[S(h,j) + S(h,j,y) \Big] \qquad *** \; \sum_{h=k}^{\ell} S(h,k-3,y,t')$$

$$** \; \sum_{m=k+1}^{k+3-1} \sum_{h=m}^{\ell} S(h,m-3,y,t') \qquad **** \; \sum_{h=k+1}^{\ell} \Big[S(h,k) + S(h,k,y) \Big]$$

Table IV: Continued

Banding Year

Sample

Observ.	1966	1967	1968	1969	1970	1971	1972
S(k,o)	401	319	357	185	40	157	269
S(k,y)	236	555	254	236	56	289	458
Sm(k)	89	135	134	160	115	143	167
S(k)	726	1009	745	581	211	589	894
*	170	265	369	406	429	326	263
**	32	69	85	45	21	42	68
***	13	15	17	15	54	31	14
****	230	238	197	138	40	104	242
Z(k)	138	196	284	361	408	284	195
R(k)	215	184	166	124	33	69	209

$$* \sum_{j=1}^{k-1} \sum_{h=k+1}^{\ell} \left[S(h,j) + S(h,j,y) \right] \qquad *** \sum_{h=k}^{\ell} S(h,k-3,y,t')$$

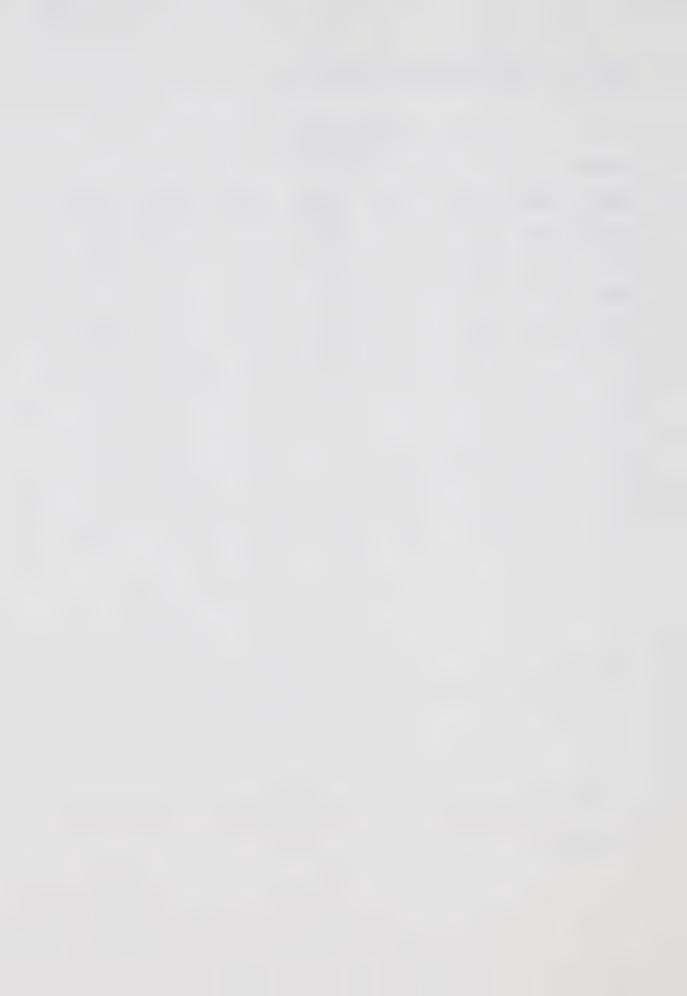$$** \sum_{m=k+1}^{k+3-1} \sum_{h=m}^{\ell} S(h,m-3,y,t') \qquad **** \sum_{h=k+1}^{\ell} \left[S(h,k) + S(h,k,y) \right]$$

Table IV: Continued

Banding Year

Sample Observ.	1973	1974	1975	1976	1977	1978	1979
S(k,o)	256	251	403	119	67	406	400
S(k,y)	367	396	705	308	250	928	677
Sm(k)	172	208	291	221	115	286	331
S(k)	795	855	1399	648	432	1620	1408
*	333	400	283	351	364	141	0
**	48	45	62	41			
***	7	35	33	15	30	32	9
****	275	174	289	128	63	190	
Z(k)	285	355	221	310			
R(k)	260	144	257	119			

$$* \sum_{j=1}^{k-1} \sum_{h=k+1}^{\ell} \left[S(h,j) + S(h,j,y) \right] \qquad *** \sum_{h=k}^{\ell} S(h,k-3,y,t')$$

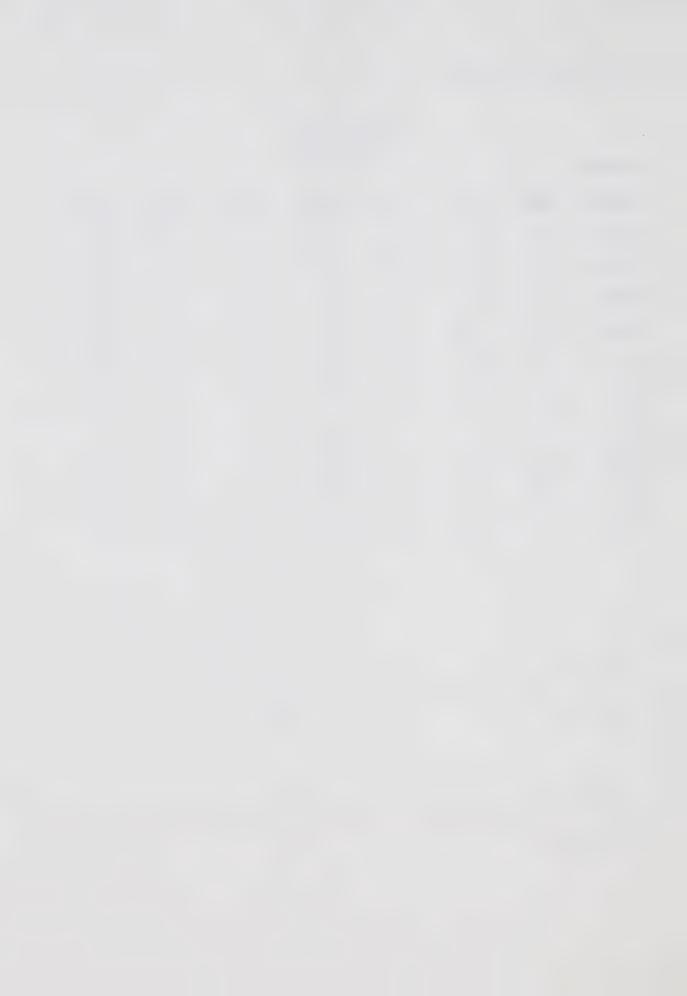$$** \sum_{m=k+1}^{k+3-1} \sum_{h=m}^{\ell} S(h,m-3,y,t') \qquad **** \sum_{h=k+1}^{\ell} \left[S(h,k) + S(h,k,y) \right]$$

Table V: Parameter Estimates

Banding Year

Para-meters	1959	1960	1961	1962	1963	1964	1965
$\hat{M}(k)$			69	110	156	279	552
$\hat{N}(k)$			773	4482	2801	3803	8134
$\hat{P}(k)$			0.10	0.14	0.35	0.09	0.13
*				0	15	0	16
$\hat{Y}(k)$	0.00	0.06	0.00	0.05	0.05	0.17	0.08
$\hat{A}(k)$			1	0.38	0.45	1	0.35
$\hat{N}(k,o)$			188	1930	1357	1698	3918
$\tilde{B}(k)$			1720	731	1302	2032	621
$\hat{N}(k,y)$			516	2442	1288	1826	3664
**			257	2040	1513	1977	4470
***			0.66	0.54	0.46	0.48	0.45

* $\hat{N}(k,k-3,y,t')$

** $\hat{M}(k) + \hat{N}(k,o)$

*** $\hat{N}(k,y) / \tilde{N}(k)$

Table V: Continued

Banding Year

Para-meters	1966	1967	1968	1969	1970	1971	1972
$\hat{M}(k)$	404	619	974	1164	2031	1378	574
$\hat{N}(k)$	3292	4624	5415	4228	3727	5675	3072
$\hat{P}(k)$	0.22	0.22	0.14	0.14	0.06	0.10	0.29
*	23	28	40	34	210	100	22
$\hat{Y}(k)$	0.14	0.38	0.39	0.09	0.18	0.29	0.13
$\hat{A}(k)$	0.73	0.99	0.85	1	0.62	0.36	0.75
$\hat{N}(k,0)$	1818	1462	2595	1346	707	1513	924
$\hat{B}(k)$	422	1456	0	673	1101	438	464
$\hat{N}(k,y)$	1070	2543	1846	1718	989	2784	1574
**	2222	2081	3569	2510	2738	2891	1498
***	0.33	0.55	0.34	0.41	0.27	0.49	0.51

* $\hat{N}(k,k-3,y,t')$

** $\hat{M}(k) + \hat{N}(k,o)$

*** $\hat{N}(k,y) / \tilde{N}(k)$

Table V: Continued

Para-	Banding Year						
meters	1973	1974	1975	1976	1977	1978	1979
$\hat{M}(k)$	641	1340	888	1107			
$\hat{N}(k)$	2964	5506	4268	3245			
$\hat{P}(k)$	0.27	0.16	0.33	0.20			
*	10	83	57	31			
$\hat{Y}(k)$	0.85						
$\hat{A}(k)$	1	0.52	0.83				
$\hat{N}(k,o)$	954	1617	1230	596			
$\hat{B}(k)$	639	517	0				
$\hat{N}(k,y)$	1369	2549	2150	1542			
**	1595	2957	2118	1703			
***	0.46	0.46	0.50	0.48			

* $\hat{N}(k,k-3,y,t')$

** $\hat{M}(k) + \hat{N}(k,o)$

*** $\hat{N}(k,y) \, / \, \hat{N}(k)$

Table VI: Clutch Sizes, Anderson River Delta

Sample Year	Number of Nests	Number of Eggs	Habitat Area Sampled (%)	Estimated Number of Young
1959	221	692	10	6920
1960	378	1518	25	6072
1961	177	697	10	6970
1962	490	1899	30	6330
1963	569	2151	40	5378
1964	131	417	10	4170
1965	490	1801	30	6003
1972	53	187	5	3740
1973	76	291	5	5820
1974	51	174	5	3480
1975	223	808	15	5387
1976	133	510	10	5100
1977	196	836	10	8360
1978	163	629	10	6290
1979	144	490	10	4900
1980	289	960	20	4800

Table VII: Distribution of Replaced Bands

Sample Year	Replaced Bands	Unetchable Bands	No. of Recaptures	Recaptures Replaced %
1959				
1960	0	0	0	
1961	0	0	0	
1962	5	0	15	33
1963	13	2	54	24
1964	3	1	26	12
1965	14	2	74	19
1966	13	1	89	15
1967	26	0	135	19
1969	18	1	160	11
1970	3	2	115	3
1972	23	0	167	14
1973	9	0	172	5
1975	17	0	291	6
1976	13	0	221	6
1977	13	0	115	11
1978	36	2	286	13
1979	24	0	331	7

Table VIII: Distribution of Banding Locations,
           Anderson River Delta

	Group 1	Group 2		
	Kettle			
Sample	Hole	Brant	Study Area	Fox Den
Year	Point	Island	Island	Island
1959	*			
1960	*			*
1961	*			
1962	*	*		
1963	*			*
1964				
1965				*
1966	*			*
1967	*			
1969	*			
1970	*			
1972	*			
1973	*			
1975	*		*	
1976	*	*		
1977	*			
1978	*			*
1979	*			*

Table VIII: Continued

Sample Year	Group 3			Group 4	
	Juncus Island	Triangle Island	Loon Channel	Middle Creek	Shearpin Creek
1959					
1960					
1961					
1962					
1963				*	
1964				*	*
1965				*	
1966					*
1967			*	*	*
1969				*	
1970					
1972				*	
1973				*	
1975					
1976	*			*	
1977				*	
1978				*	*
1979	*				*

Table IX: Use of Molting Sites by Brant,
Anderson River Delta

Recapture Area

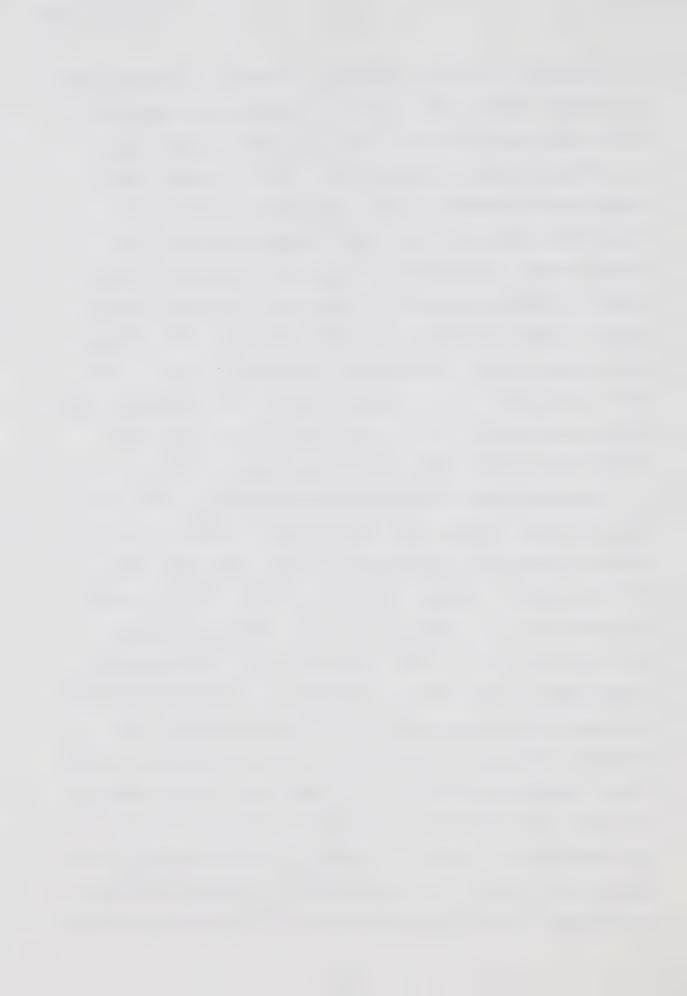| Capture Area	Kettle Hole Point	FoxDen Island	Triangle Island	Middle Creek
Kettle Hole Point	365	202	48	61
FoxDen Island	87	162	62	84
Triangle Island	14	15	6	5
Middle Creek	92	68	24	463

D. Discussion

This analysis of the banding data of the Anderson River brant provides reasonable parameter estimates. My results indicate that the number of adult brant $(N(k,o) + M(k))$ breeding in the delta ranged from a low of 1513 to a high of 4470, with a mean value of 2390. This interval encompasses the estimated population size of 3000 for this colony (Barry, 1967). Barry's figure was derived from direct observation, clutch-sizing operations, and aerial surveys during a period of years overlapping with this study.

My mean estimated yearly production of young $(N(k,y))$ is 1957, substantially less than the possible number of young produced from eggs at Anderson River each year (Table V). However, this colony has a high egg and chick loss due to predation and natural mortality prior to banding season (pre-fledged stage)(Martin and Barry, 1973; Barry and Barry, in press). A mean production of 5600 eggs is reduced by 23% to 27% (these percentages are the result of clutch size studies on brant in other areas), (Bellrose, 1976; Palmer, 1976; Pacific Waterfowl Flyway Council, 1978) to about 4000 successfully hatched and dried chicks. Furthermore, during the next three weeks prior to fledging, these survivors are further reduced in number by about 30% to 35% (Barry, pers. comm.; Bellrose, 1976), leaving only about 2600 young available for banding. Further assessment of my estimated number of young is made by examining the yearly percentage of young produced by the Anderson River brant, derived from

the estimates for N(k,y) and N(k), a quantity ranging from 26% to 55% (mean of 45%). This is substantially above the 10% to 40% range found for the total Pacific population (Pacific Waterfowl Flyway Council, 1978). However, local conditions at Anderson River, such as early snow melt relative to the brant's arrival, longer daylight, less precipitation, and generally more clement weather, could favour a higher percentage of young to be produced there than at other colonies, e.g. Yukon-Kuskoquim delta (Barry, pers. comm.; 1967). Furthermore, estimates of adult young ratios are made in the winter, after the fall migration and after natural mortality and hunting harvests have taken their toll (Pacific Waterfowl Flyway Council, 1978).

Analyzing band returns of brant breeding in the Yukon Delta, Alaska, Hansen and Nelson (1957) arrived at a 45.4% mortality rate for young brant in their first year. They also reported an average mortality rate of 32.2% for each succeding year. In terms of survival, these figures are equivalent to 25.1% of the young surviving the three years to adulthood. Their result is substantially higher than the 15% mean survival rate resulting from my analysis. The mortality figures of Hansen and Nelson are, however, derived from a simple deterministic life table method developed by Bellrose and Chase (1950) who express the mortality rate as the proportion of banded birds which died during the year as determined by bands returned by hunters and bands found on dead birds. The obvious deficiencies of this method are that

not all band recoveries are reported by hunters and certainly not all dead birds with bands are found: that is, dead *banded* birds are found with a lower probability than the dead *unbanded* birds, since there are relativly few marked birds in the population. This bias results in an underestimate of the actual mortality rate, ie., an overestimate of the survival rate.

For the adult survival probability a more reliable estimate than that provided by Hansen and Nelson is given by Boyd (in Le Cren and Holdgate, 1962) and lends credence to my estimated survival rate of 0.70. Boyd applied an estimation technique, developed by Haldane (described in Seber, 1973), to the banding data of Hansen and Nelson and found that their Alaskan brant had a constant survival rate of 0.85. Using banding data collected in Spitzbergen, Boyd also calculated that the closely related Atlantic brant survived with a probability of 0.83. Haldane's stochastic estimation procedure is more credible than that of Bellrose and Chase since he at least included in his analysis a constant probability that a band is found and reported. However, Haldane's method is not completely realistic, since this probability could change with hunting pressure and banding effort; for the purpose of comparison though, Boyd's estimates will be sufficient.
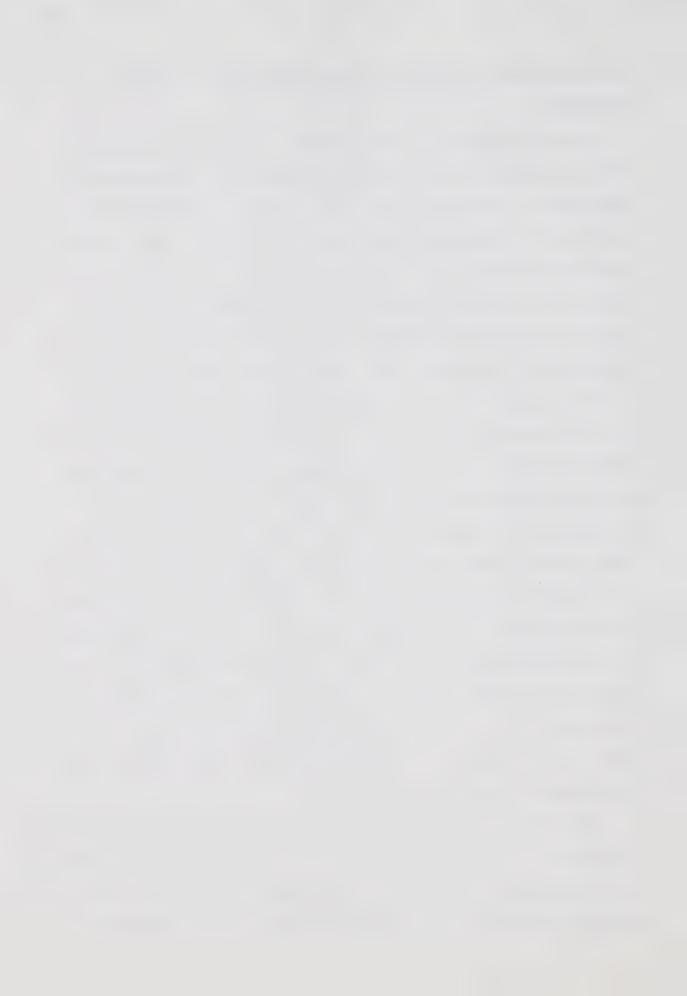
The remaining population parameters are $N(k,k-3,y,t)$, the number of three year old adults, and $B(k)$, the number of recruits. There are no estimates of these parameters from

other sources with which to draw comparisons or make assessments.

Several aspects of the assumptions must be examined in order to ascertain the validity of applying the estimation equations to this particular set of data. As noted in the results, the Anderson River brant are likely to use the same specific molting areas (these being Kettle Hole Point, Fox Den Island, Triangle Island and Middle Creek) within the delta from season to season. It is evident then that the marked geese, released after each season's banding drives, do not thoroughly mix with the remainder of the population by the following year or, for that matter, possibly ever. In addition, there were different sampling techniques employed during the course of the study (boat or helicopter). The concentration of sampling in only a few areas versus the later general sampling by helicopter causes problems. It is very probable that not all of the Anderson River brant have the same probability of being captured in any one season and that the sampling is, in effect, non-random. Brant that are banded on Fox Den Island or Triangle Island, for example, might have little or no chance of being recaptured if that site is not resampled in subsequent years, even though the birds may be present in the delta.

The effect of this non-random sampling on the estimates is twofold. Intuitively, the estimates of the survival rates of both young and adults will be biased on the low side if enough individuals are involved in one of the infrequently

used banding sites. Since the survival rates are basically
estimated by the proportion of marked birds that survive to
and are captured in the next sampling period (third next for
the young), it is clear that this estimation procedure will
interpret the event 'a greater number of marked birds not
being recaptured due to non-random sampling' as the event
that 'more of these marked birds are dying before they are
recaptured'. As a result of this misinterpretation a lower
estimate of the probability of surviving is produced.
Secondly, the estimates of the population size will be
inflated since more marked geese could potentially be
captured if the sampling were random; the estimation
procedure translating (see equation (14)) the event 'reduced
proportion of marked in the sample' as the event that 'more
geese are in the population'. This results in an estimate
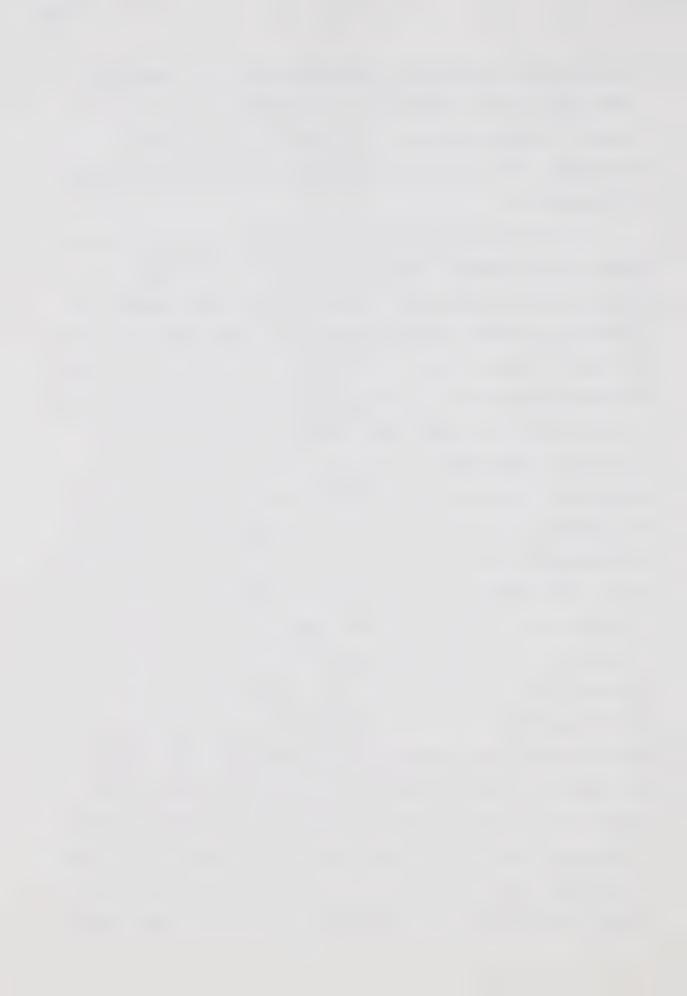that is biased on the high side.

Another source of error in applying these estimation
results to this specific population is that assumption 5 is
violated: geese do not lose their bands during the course of
the study. The rough estimate for the rate of band
replacement and band life represents minimum values for
these statistics and suggests that the band loss is very
high from year to year. When the softer aluminum bands were
used, 11% to 33% of the recaptured aluminum bands had to be
replaced each year. That this problem occurs and complicates
the data analysis is very certain, the ramifications of such
high loss being inflated population estimates and deflated

survival rates caused by a reduced proportion of marked individuals in the population. The reasoning of this argument follows exactly that given in the previous discussion, the effect of band loss and non-random sampling are identical.

A further problem affecting the analysis of this brant population is that on the spring migration the recently matured males follow their females to the colony where she originally hatched, seldom returning to the colony where the male was hatched. Thus at the Anderson River there is a loss of banded males and a corresponding influx of unbanded males following the returning local females. This results in a dilution of the supply of marked birds and hence biased estimates. Examination of band returns has shown that such an exchange exists between the brant breeding in Alaska and at Anderson River (Barry, 1959 to 1979) and is also known to occur with populations of snow geese (*Chen hyperborea*) (Cooke et al., 1975; Finney and Cooke, 1978).

I will also mention in passing (and without any direct evidence) that there is a distinct possibility that the tacit assumption of brant always breeding at age three may not be valid. While preparing the banding data for Tables I, II, and III, I noticed that during the last three to four years of the banding program a significantly higher number of one- and two-year-old geese were being recaptured for the first time, but that overall, there was a tendency for the young brant to be first recaptured five, six, or more years

later.

Conclusions

To briefly summarize, I have addressed the problem of
estimating parameters of a non-homogeneous population
consisting of two recognizable age groups, adult and young,
where the latter require some specified constant number of
years (r) in which to attain adult status. The estimation
procedure derived for this type of population allows for one
probability that the young survive this maturing phase and a
different probability that the adults survive the one year
intervals thereafter. The estimates of population parameters
are found by maximum likelihood techniques.

In theory, the area of applicability of this estimation
scheme are those populations not covered by Pollock's
general analysis discussed earlier. This includes those
species of birds, mammals, fish, *et cetera*, in which the
subadult members may or may not be distinguishable from the
adults but they at least spend the breeding season in areas
away from the adults (that is, if marking takes place during
the breeding season). In practice, however, there are
several factors which severely limit the extent to which
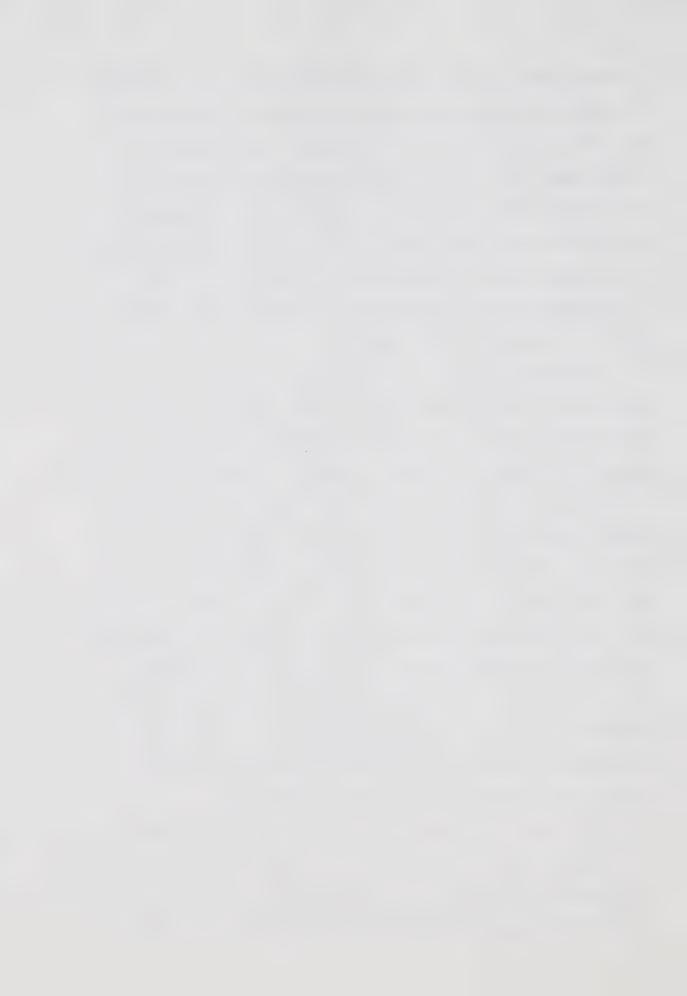this analysis will or could be used.

Primarily, in this procedure, more time required for
the young to mature, that is, larger values of r. will
require more samples to be taken. This is because the number
of samples must be at least r before any calculations can be
made at all. Furthermore, for any reasonable measure of

accuracy and reliability to be attained in the estimates, the marking program must be continued for a substantial period of time after the r'th sample, resulting in a requirement for a large body of capture-recapture data. Satisfying this requirement presents many problems with conflicting solutions when dealing with a species for which the young require a long maturation period; accuracy requirements must be balanced with the available study time and the urgency of the situation.

Perhaps even more restricting in terms of the applicability of my analysis is that there are relatively few species which can be easily captured on a scale large enough to allow sufficiently sizeable numbers of individuals to be marked. There are even fewer species of this type whose populations follow the pattern required for this analysis. This estimation procedure is designed to be applied primarily to geese, about the only species meeting the specifications discussed above. However this designed application may be limited as well. For the forseeable future the era of long term observational investigations is drawing to a close as government funds for these types of studies are curtailed and even withdrawn completely in favour of investigations of shorter duration.

The results of applying this estimation procedure to the capture-recapture data of the Anderson River brant are sufficient to determine that the estimation equations are generating reasonable estimates that are near values

predicted through experience and from other sources. For use in management programs, however, the reliability of my results are not completely satisfying. This is, to a large extent, due to the lack of consistency in data collection procedures and to the presence of three years of missing data. Recommendations for further studies then would include a designed sampling method that would provide consistent sample sizes and would be adaptable to idiosyncrasies of the population in question. As well, effort should be expended to insure that tag loss is kept to a minimum.

There are several inadequacies with the estimation procedure as I have derived it in Part I. No accounting has been given for the possibility that the survival probabilities are dependent on an individual's capture history. For example the young brant that are captured and marked are released under a great deal of stress having spent up to four hours under cold conditions in the pen, after being somewhat trampled by the flock as they are are hazed into the catch pen. On release the young often run away in many different directions, becoming widely scattered and separated from the parents and thus are easy prey for the glaucous gull (*Larus hyperboreus*) (Barry, pers. comm.; Barry and Barry, in press). Obviously these young must have a significantly lower probability of surviving than the young which did not undergo this trial.

Related to this factor of a capture-history-dependent survival rate is the very real possibility that capture

probability is not only time dependent but capture history dependent as well. A clear example of this is the white-fronted goose (*Anser albifrons*). When banding molting sub-adults in their traditional flocks, it is often very difficult to capture many if that site was sampled in the previous year. On several occasions, a helicopter and a boat as well as several people on foot were all used to herd with the result that only a few tens of the 500 or so geese were actually forced into the pen, the rest disappearing, being led by the more experienced previously marked birds.
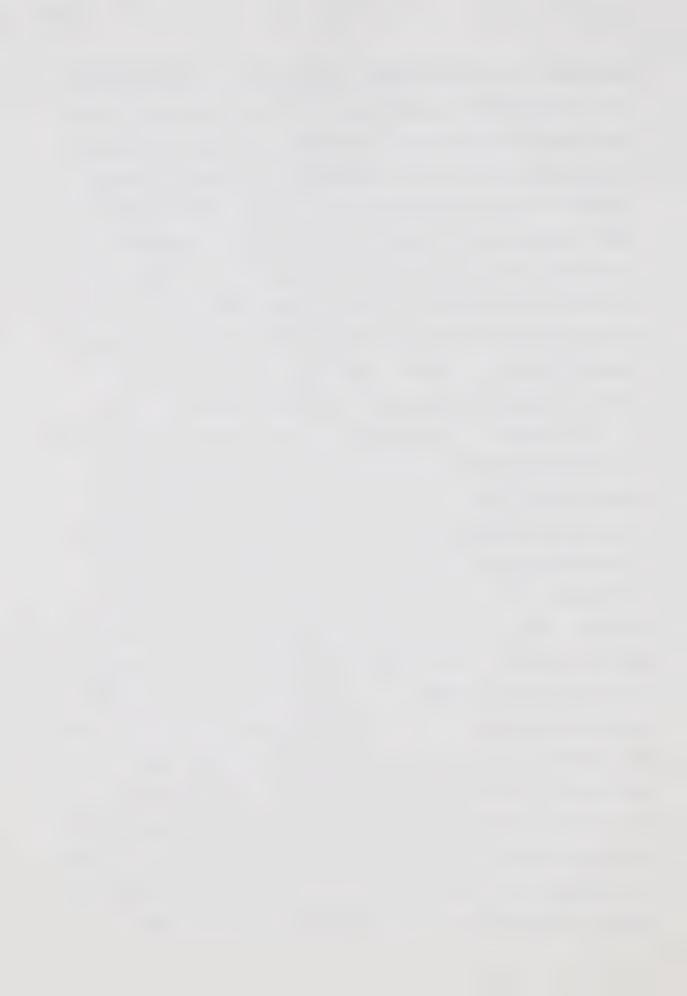
Incorporation of these two options into the analysis is, in essence, measuring the effect that the observer (the bander) has on his experiment (the geese), an endeavour which can not succeed. Since the act of observing (taking samples) itself drastically affects what the experimenter will observe, it is uncertain as to whether the parameter estimates are representative of an artificial population that is created by the observer's presence or whether the observations are made from the real population. In other words, what type of reality is being measured. This is the major problem confronting this sort of analysis, and is one that appears to be ignored by other researchers employing the Jolly-Seber type of approach.

Also neglected is any method for calculating variances and covariances of the estimates. Jolly (1965) produces variance estimates for parameters of his homogeneous population analysis by using a truncated Taylor series
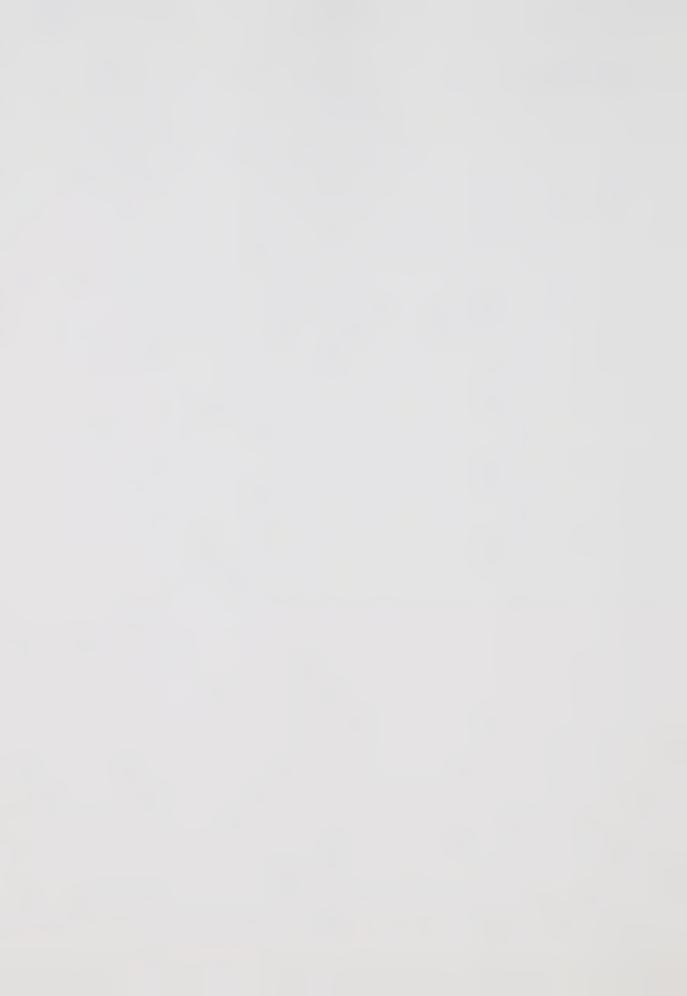
approximation. Stokes (1980) and Pollock (in press) both use this same method of approximation in their analyses, and at the present time it seems to be the only means available for computing variances in this stochastic estimation setting The main criticism and objection to using and relying on these approximate variances is that they are asymptotic, requiring a very large sample size in order to return any accuracy. Furthermore, for small sample sizes the distribution of the maximum likelihood estimators are quite skewed (Robson, in Johnson and Smith, 1968) leading to inappropriate and misleading confidence bounds.

Still open to investigation is the possibility that the estimation procedures may be improved by using data from other sources. One option is to combine the recovery type procedures of Brownie et al. (1978), which I discussed in the introduction, with the recapture method which I have developed in Part I. This would use the large body of recovery data collected for most species of North American geese and ducks. The estimation analysis could be modified to differentiate between natural mortality and that induced by hunting pressure, by introducing probabilities that young and adults survive the annual hunting barrage in the fall and winter. As well, the shot death of a banded goose definitely terminates development of the band's associated capture history vector and so precludes any possibility that the band is ever recaptured. This certainty of information should have beneficial ramifications on the existing

estimates.

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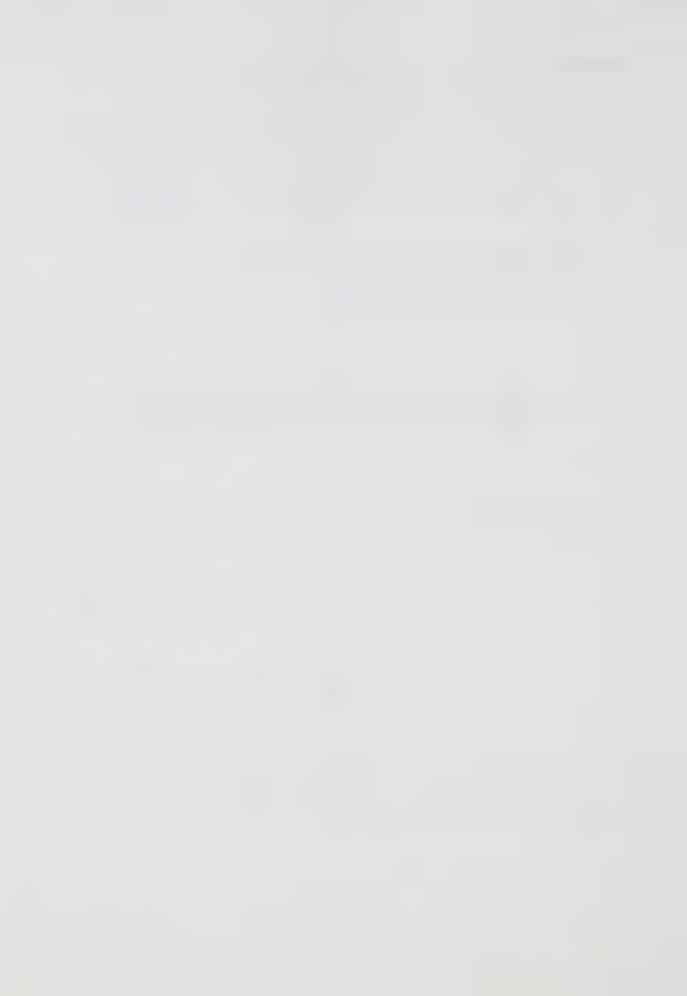
Appendix: Derivation of Estimation Equations

I will now continue with the derivation of the estimation equations following the derivation of equation (12) in Part I. The final versions of these subsequent equations are given as (13) through (20) at the end of Part I.

The number of unmarked adults at time k has the following likelihood function:

$$L(N_{ko}) = \frac{K (1-P_k)^{N_{ko}} (1-A_k)^{N_{ko}} A_{k-1}^{N_{ko}} (1-A_{k-1})^{-N_{ko}} N_{ko}!}{(N_{ko}-B_{k-1})! (N_{ko}-S_{ko}-N_{k+1o}+B_k)! (N_{k-1o}-S_{k-1o}-N_{ko}+B_{k-1})!}$$

Then $\Delta \ln(L(N_{ko})) = \ln(1-P_k) + \ln(1-A_k) + \ln(A_{k-1}) - \ln(1-A_{k-1}) +$

$$\ln(N_{ko}) - \ln(N_{ko}-B_{k-1}) - \ln(N_{ko}-S_{ko}-N_{k+1o}+B_k) +$$

$$\ln(N_{k-1o}-S_{k-1o}-N_{ko}+B_{k-1}+1).$$

Setting $\Delta \ln L(N(k,o)) = 0$ and using equation (12) for $B(k)$ and $B(k-1)$ and solving for $N(k,o)$:

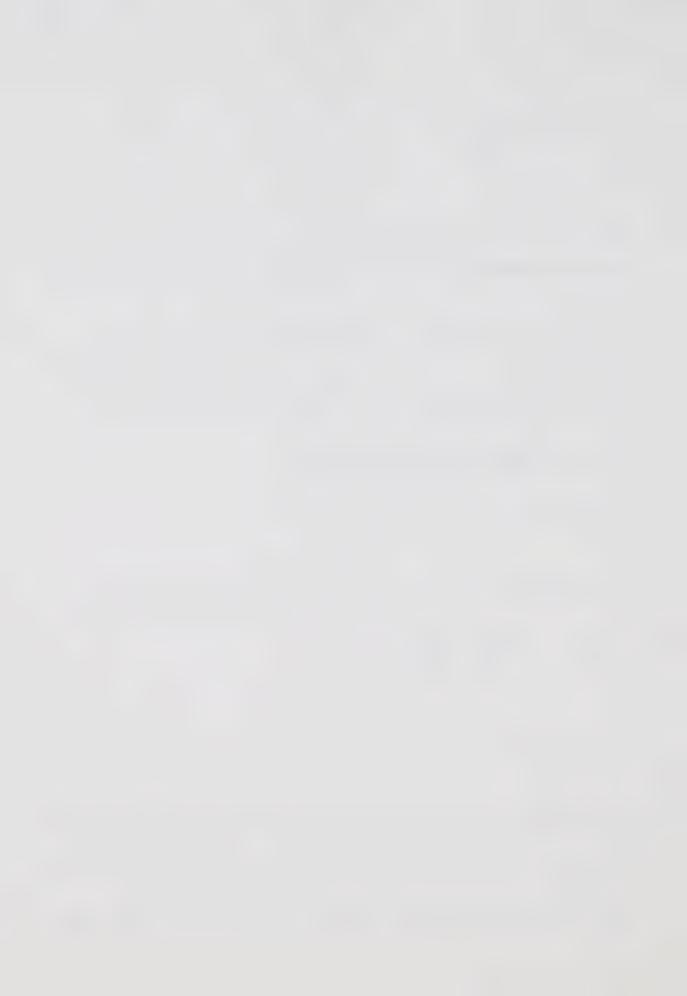(A1) $\hat{N}_{k0} = \dfrac{S_{k0}}{\hat{P}_k}$,

for $k = 1, \ldots, \ell$.

Thus the number of unmarked adults is estimated by the
number of unmarked adults in the sample inflated by a factor
of $1/P(k)$.

Using the estimate of the number of recruits, $B(k)$,
from equation (12) the estimate of $A(k)$, the adult survival
rate, given by equation (11) is revised as follows:

$$\hat{A}_k = \dfrac{\hat{N}_{k+1} - \hat{N}_{k+1y} - \hat{N}_{k+1 0} - \hat{N}_{k+1\,k+1-ryt}}{\hat{N}_k - \hat{N}_{ky} - \hat{N}_{k0} + S_{k0}} ,$$

for $k = r, \ldots, (\ell-r-1)$.

which reduces to the following after using equation (1):

(A2) $\hat{A}_k = \dfrac{\hat{M}_{k+1} - \hat{N}_{k+1\,k+1-ryt}}{\hat{M}_k + S_{k0}}$,

for $k = r, \ldots, (\ell-r-1)$.

This estimate finds the proportion of those marked adults at
time k who have survived to time (k+1). The number of young
that became adults at time (k+1) are removed from the
numerator as they were not members of the marked population

at time k.

From (8) the likelihood function of the young at time k
is:

$$L(N_{ky}) = \frac{k(1-P_k)^{N_{ky}} N_{ky}!}{(N_{ky} - S_{ky})!} \quad,$$

for $k = r, \ldots, (\ell-r)$.

and

$$\Delta \ln L(N_{ky}) = \ln(1-P_k) + \ln(N_{ky}) - \ln(N_{ky} - S_{ky})$$

and setting $\Delta \ln L(N(k,y)) = 0$ gives:

$$(A3) \quad \hat{N}_{ky} = \frac{S_{ky}}{\hat{P}_k} \quad,$$

for $k = r, \ldots, (\ell-r)$.

Like the unmarked adults, $N(k,y)$ is the number of young in
the k'th sample scaled up by an ammount $1/P(k)$.

The likelihood of the number of young that are just
becoming adults is:

$$L(N_{kk-ryt}) = \frac{k(1-P_k)^{N_{kk-ryt}}(1-A_k)^{N_{kk-ryt}} Y_{k-r}^{N_{kk-ryt}} (1-Y_{k-r})^{-N_{kk-ryt}} N_{kk-ryt}!}{(S_{k-ry} - N_{kk-ryt})! \, N_{kk-ryt}! \, (N_{kk-ryt} - S_{kk-ryt} - N_{k+1k-ryt'})!}$$

for $k = (r+1), \ldots, (\ell-1)$.

Again, by setting the first difference of the logarithm to zero, one gets:

$$(A4) \quad \frac{S_{k-ry} - \hat{N}_{kk-ryt}}{\hat{N}_{kk-ryt} - S_{kk-ryt} - \hat{N}_{k+1k-ryt'}} = \frac{(1 - \hat{Y}_{k-r})}{(1 - \hat{P}_k)(1 - \hat{A}_k)\hat{Y}_{k-r}} \quad ,$$

for $k = (r+1), \ldots, (\ell-1)$.

since the relative error in equating $N(k,k-r,y,t) - 1$ to $N(k,k-r,y,t)$, for large $N(k,k-r,y,t)$, is negligible. This may be rewritten as:

$$(A5) \quad \hat{N}_{k+1k-ryt'} = \hat{N}_{kk-ryt} - S_{kk-ryt} -$$

$$\left[\frac{(1 - \hat{P}_k)(1 - \hat{A}_k)\hat{Y}_{k-r}}{(1 - \hat{Y}_{k-r})}\right] \cdot \left[S_{k-ry} - \hat{N}_{k,k-ryt}\right] \quad ,$$

for $k = (r+1), \ldots, (\ell-1)$.

Two further relations, required for some later estimates, are derived below.

From (1)

$$\hat{N}_k = \hat{N}_{ky} + \hat{N}_{ko} + \hat{M}_k \quad , \quad \text{for } k = 1, \cdots, \ell.$$

$$= \frac{S_{ky}}{\hat{P}_k} + \frac{S_{ko}}{\hat{P}_k} + \hat{M}_k$$

$$= \frac{S_{ky}}{S_k}\hat{N}_k + \frac{S_{ko}}{S_k}\hat{N}_k + \hat{M}_k$$

So that using (2),

$$\frac{\hat{N}_k}{S_k} S_{mk} = \hat{M}_k$$

Then

$$(A6) \quad \frac{\hat{N}_k}{S_k} = \frac{\hat{M}_k}{S_{mk}} \quad \text{or} \quad \hat{P}_k = \frac{S_{mk}}{\hat{M}_k}$$

for $k = 1, \cdots, \ell$.

Several estimation equations will now be extracted from the likelihood function (8). By combining these with some previous equations an estimate for N(k+1,k) + N(k+1,k,y) will be found.

Firstly, estimates of those adults last captured at some previous time 'j' and initially marked when adults, will be made.

There are two cases to consider:

1) For j = 1 . . . (k-2) and all capture histories w the likelihood function is:

$$L(N_{kjw}) = \frac{K \; (1-P_k)^{N_{kjw}} \; (1-A_k)^{N_{kjw}} \; A_{k-1}^{N_{kjw}} \; (1-A_{k-1})^{-N_{kjw}} \; N_{kjw}!}{N_{kjw}! \; (N_{kjw} - S_{kjw} - N_{k+1jr})! \; (N_{k-1jw} - S_{k-1jw} - N_{kjw})!} \quad ,$$
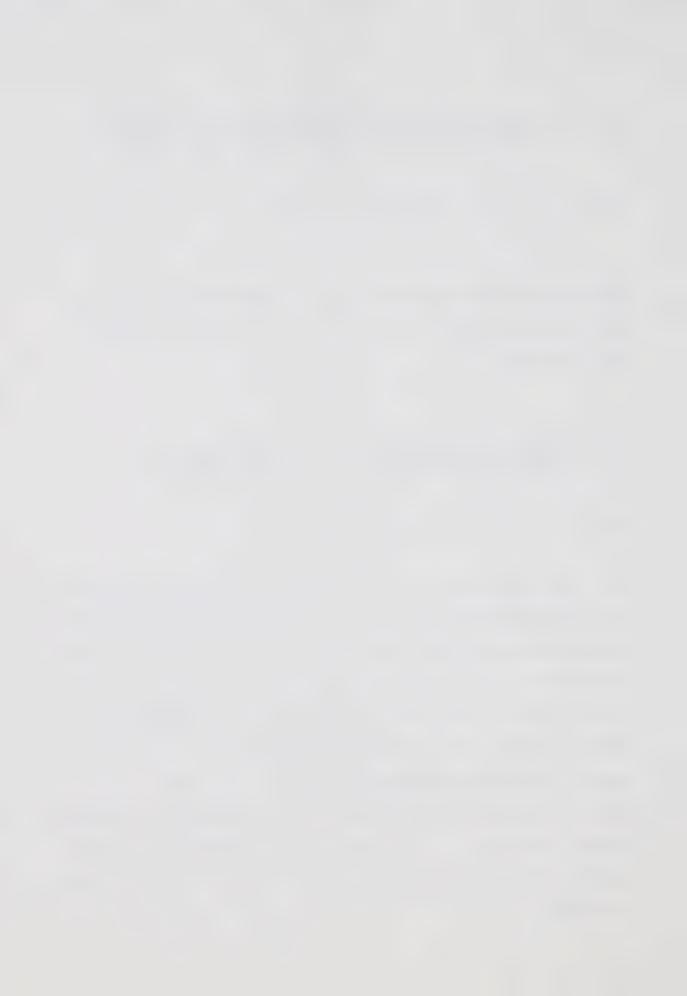
for $k = r, \ldots, (\ell-1)$ and $j = 1, \ldots, (k-2)$.

Setting the first difference of the logarithm of this to zero and replacing $N(k,j,w) - 1$ with $N(k,j,w)$ for large $N(k,j,w)$ gives:

$$(A7) \quad \frac{\hat{N}_{k-1jw} - S_{k-1jw} - \hat{N}_{kjw}}{\hat{N}_{kjw} - S_{kjw} - \hat{N}_{k+1jr}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}} \quad ,$$

for $k = r, \ldots, (\ell-1)$ and $j = 1, \ldots, (k-2)$.

The right hand side of (A7) is a ratio of probabilities and the left hand side is a ratio of the corresponding expected frequencies within the class of $N(k-1,j,w)$. Intuitively the numerator of the left hand side of (A7) considers the adults at time $(k-1)$ (last captured at time j) and removes all members of this group who were captured in the $(k-1)'$th sample (these would become $N(b,k-1,w')$ for some $b > (k-1)$) and then removes those members of this group who survived to time k ($N(k,j,w)$). This then leaves those which did not survive to time k - analogous to ($1 - A(k)$) in the right hand side.

A description of the intuitive equivalence between the denominators is similar. The proportion of N(k-1,j) that survive to time k and and form the N(k,j,w) is A(k-1). (1-P(k)) is the probability that these survivors will not be captured, and so those that were captured (S(k,j,w)) must be removed from the left side. These uncaptured survivors die with probability (1-A(k)) before time (k+1). The survivors (N(k+1,j,v)) are therefore removed from the left side maintaining the equivalence.

2) When j = (k-1) there are two forms of the capture history w to consider.

a) When w has the form of q, (w = (0,0,...,0,1)), then:

$$L(N_{k\,k-1w}) = \frac{K\,(1-P_k)^{N_{kk-1w}}\,(1-A_k)^{N_{kk-1w}}\,A_{k-1}^{N_{kk-1w}}\,(1-A_{k-1})^{-N_{kk+w}}\,N_{kk-1w}!}{(S_{k-10}-N_{kk-1w})!\,N_{kk-1w}!\,(N_{kk-1w}-S_{kk-1w}-N_{k+1\,k-1v})!}\,,$$

for $w = q$ and $K = r,\ldots,(\ell-1)$.

Again since the relative error of estimating N(k,k-1,w) - 1 by N(k,k-1,w) is negligible for large N(k,k-1,w), setting the first difference to zero will result in:

$$(A8) \quad \frac{S_{k-1 0} - \hat{N}_{k k-1 w}}{\hat{N}_{k k-1 w} - S_{k k-1 w} - \hat{N}_{k+1 k-1 v}} = \frac{(1 - \hat{A}_{k-1})}{(1 - \hat{P}_k)(1 - \hat{A}_k) \hat{A}_{k-1}} ,$$

for $w = q$ and $k = r, \ldots, (l-1)$.

b) When w has any form other than q, then:

$$L(N_{k k-1 w}) = \frac{K (1 - P_k)^{N_{k k-1 w}} (1 - A_k)^{N_{k k-1 w}} A_{k-1}^{N_{k k-1 w}} (1 - A_{k-1})^{-N_{k k-1 w}} N_{k k-1 w}!}{N_{k k-1 w}! \left(\sum\limits_{j=1}^{k-1} S_{k-1 j w} - N_{k k-1 w} \right)! (N_{k k-1 w} - S_{k k-1 w} - N_{k+1 k-1 v})!} ,$$
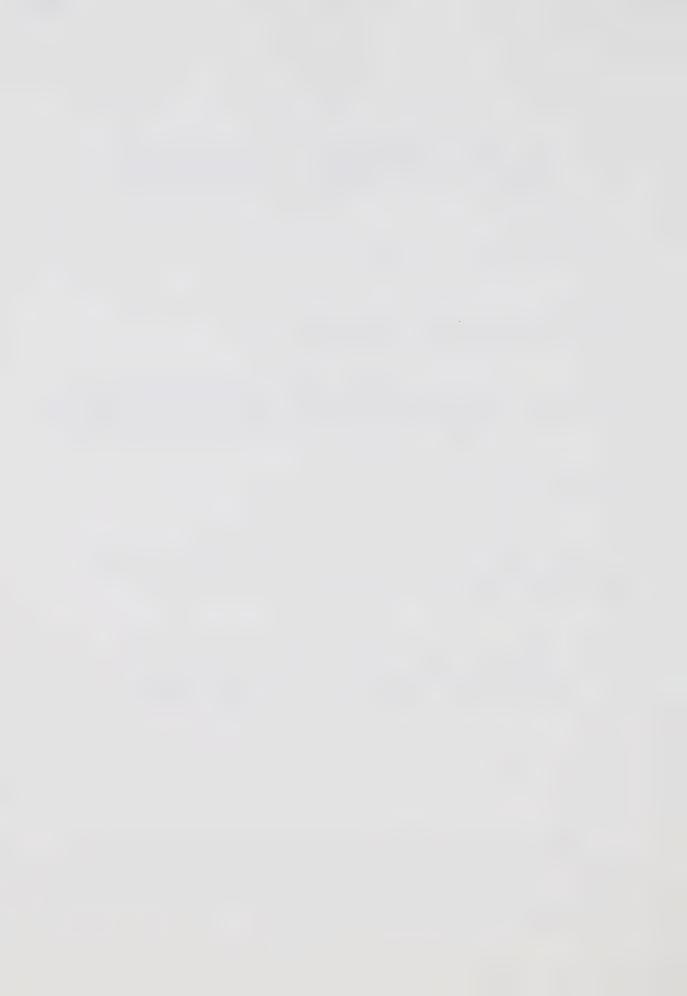
for $k = r, \ldots, (l-1)$

and, for large N(k,k-1,w), the first difference of the logarithm of the likelihood set to zero will give:

$$(A9) \quad \frac{\sum\limits_{j=1}^{k-1} S_{k-1 j w} - \hat{N}_{k k-1 w}}{\hat{N}_{k k-1 w} - S_{k k-1 w} - \hat{N}_{k+1 k-1 v}} = \frac{(1 - \hat{A}_{k-1})}{(1 - \hat{P}_k)(1 - \hat{A}_k) \hat{A}_{k-1}} ,$$

for $k = r, \ldots, (l-1)$.

Next, estimation equations for those adults initially marked as young are developed. As with the adults marked as adults there are two cases to consider.

a) For j = 1, . . . ,(k-2), except for the case j = (k-r) and w = t, the likelihood function is:
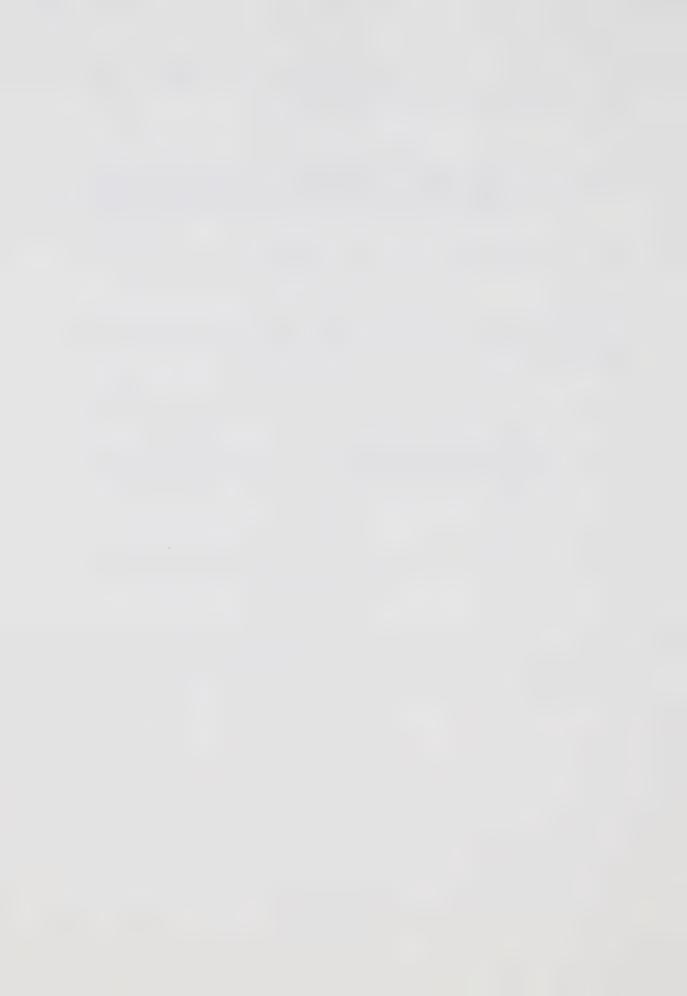
$$L(N_{kjyw}) = \frac{K\ (1-P_k)^{N_{kjyw}}(1-A_k)^{N_{kjyw}}A_{k-1}^{N_{kjyw}}(1-A_{k-1})^{-N_{kjyw}}N_{kjyw}!}{N_{kjyw}!\ (N_{kjyw}-S_{kjyw}-N_{k+1jyv})!\ (N_{k-1jyw}-S_{k-1jyw}-N_{kjyw})!}\ ,$$

for $k = r, \cdots, (\ell-1)$ and $j = 1, \cdots, (k-2)$ except for $j = (k-r)$ when $w = t$.

For large N(k,j,y,w) the maximum likelihood equation, upon setting $\triangle$ ln L(N(k,j,y,w) to zero becomes:

$$(A10)\qquad \frac{\hat{N}_{k-1jyw}-S_{k-1jyw}-\hat{N}_{kjyw}}{\hat{N}_{kjyw}-S_{kjyw}-\hat{N}_{k+1jyr}}\ =\ \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}}\ ,$$

for $k = r, \cdots, (\ell-1)$ and $j = 1, \cdots, (k-2)$ except for $j = (k-r)$ when $w = t$.

b) When j = (k-1) and w has any other form, the likelihood equation is:

$$L(N_{k\,k-1y\omega}) = \frac{K\,(1-P_k)^{N_{k\,k-1y\omega}}\,(1-A_k)^{N_{k\,k-1y\omega}}\,A_{k-1}^{N_{k\,k-1y\omega}}\,(1-A_{k-1})^{N_{k\,k-1y\omega}}\,N_{k\,k-1y\omega}!}{N_{k\,k-1y\omega}!\,(N_{k\,k-1y\omega}-S_{k\,k-1y\omega}-N_{k+1\,k-1yv})!\,(\sum_{j=1}^{k-2}S_{k-1jy\omega}-N_{k\,k-1y\omega})!},$$

for $k = 1, \ldots, (\ell-1)$.

For large $N(k,k-1,y,w)$, setting $\triangle\ln L(N(k,k-1,y,w)$ to zero results in:

(A11)
$$\frac{\sum_{j=1}^{k-2}S_{k-1jy\omega}-\hat{N}_{k\,k-1y\omega}}{\hat{N}_{k\,k-1y\omega}-S_{k\,k-1y\omega}-\hat{N}_{k+1\,k-1y\omega}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\,\hat{A}_{k-1}},$$

for $k = 1, \ldots, (\ell-1)$.

The intuitive description of the equations (A8), (A9), (A10) and (A11) will follow that given for (A7) with few modifications.

Since the right hand side of equations (A7) through (A11) are independent of the capture histories w, the numerators and denominators of each of these equations are summed separately over all capture histories w. This results in the following equations:

$$(A12) \quad \frac{\hat{N}_{k-1j} - S_{k-1j} - \hat{N}_{kj}}{\hat{N}_{kj} - S_{kj} - \hat{N}_{k+1j}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}} \quad ,$$

for $k = r, \ldots, (\ell-1)$ and $j = 1, \ldots, (k-2)$.

$$(A13) \quad \frac{S_{k-10} - \hat{N}_{kk-1}}{\hat{N}_{k_T k-1} - S_{kk-1} - \hat{N}_{k+1\,k-1}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}} \quad ,$$

for $k = r, \ldots, (\ell-1)$.

$$(A14) \quad \frac{\sum_{j=1}^{k-2} S_{k-1j} - \hat{N}_{kk-1}}{\hat{N}_{kk-1} - S_{kk-1} - \hat{N}_{k+1\,k-1}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}} \quad ,$$

for $k = r, \ldots, (\ell-1)$.

$$(A15) \quad \frac{\tilde{N}_{k-1jy} - S_{k-1jy} - \hat{N}_{kjy}}{\tilde{N}_{kjy} - S_{kjy} - \tilde{N}_{k+1jy}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}} \quad ,$$

for $k = r, \ldots, (\ell-1)$ and $j = 1, \ldots, (k-2)$ except for $j = (k-r)$ when $w = t$.

$$(A16) \quad \frac{\sum_{j=1}^{k-2} S_{k-1jy} - \hat{N}_{kk-1y}}{\hat{N}_{kk-1y} - S_{kk-1y} - \hat{N}_{k+1\,k-1y}} = \frac{(1-\hat{A}_{k-1})}{(1-\hat{P}_k)(1-\hat{A}_k)\hat{A}_{k-1}} \quad ,$$

for $k = r, \ldots, (\ell-1)$.

Since each right hand side of (A12) through (A16) is independent of j all of the terms in the numerators, dependent on j, can be summed over the range of j for j = 1, . . . ,(k-2). Similarly, all terms in the denominators are summed over j, resulting in five equations. These five are reduced to one by adding the numerators together and adding the denominators together and equating the result to the right hand side. Equation (A15) is not valid, however when j = (k-r) and w = t and so, this equation must be removed in the final analysis. Even though the denominators of (A13) and (A14) are the same, they must not be counted twice as they were derived from two different forms of capture histories.

Manipulating (A12) to (A16) in the manner described above will give:

$$\frac{\sum_{j=1}^{k-2} \hat{N}_{k-1j} - \sum_{j=1}^{k-2} S_{k-1j} - \sum_{j=1}^{k-2} \hat{N}_{kj} + S_{k-10} - \hat{N}_{kk-1} + \sum_{j=1}^{k-2} S_{k-1j} + \sum_{j=1}^{k-2} \hat{N}_{k-1jy} - \sum_{j=1}^{k-2} S_{k-1jy} - \sum_{j=1}^{k-2} \hat{N}_{kjy} + \sum_{j=1}^{k-2} S_{k-1jy} - \hat{N}_{kk-1y} - \hat{N}_{k-1k-ryt} + S_{k-1k-ryt} - \hat{N}_{kk-ryt}}{\sum_{j=1}^{k-2} \hat{N}_{kj} - \sum_{j=1}^{k-2} S_{kj} - \sum_{j=1}^{k-2} \hat{N}_{k+1j} + \hat{N}_{kk-1} - S_{kk-1} - \hat{N}_{k+1k-1} + \sum_{j=1}^{k-2} \hat{N}_{kjy} - \sum_{j=1}^{k-2} S_{kjy} - \sum_{j=1}^{k-2} \hat{N}_{k+1jy} + \hat{N}_{kk-1y} - S_{kk-1y} - \hat{N}_{k+1k-1y} - \hat{N}_{kk-ryt} + S_{kk-ryt} + N_{k+1k-ryt'}}$$

$$= \frac{(1 - \hat{A}_{k-1})}{(1 - \hat{P}_k)(1 - \hat{A}_k)\,\hat{A}_{k-1}}\quad,$$

for $k = r, \ldots, (\ell-1)$.

The last three terms in the numerator and the denominator account for the case j = (k-r) and w = t from equation (A10).

Using the relation (1), the numerator reduces to

$$\hat{M}_{k-1} + S_{k-10} - \hat{M}_k + \hat{N}_{k\,k-ryt}$$

since N(k-1,k-r,y,t) = S(k-1,k-r,y,t) = 0 (these are still young and are assumed to be out of the population).

The denominator is similarly rearranged and after adding and subtracting N(k+1,k) + N(k+1,k,y) becomes:

$$\hat{M}_k - S_{mk} - \hat{M}_{k+1} - \hat{N}_{k\,k-ryt} + S_{k\,k-ryt} + \hat{N}_{k+1\,k-ryt}' + \hat{N}_{k+1\,k} + \hat{N}_{k+1\,ky}$$

And so, the equation relating the ratio of probabilities to the ratio of the corresponding expected frequencies becomes:

$$(A17) \quad \frac{\left[\hat{M}_{k-1} + S_{k-10}\right] - \left[\hat{M}_k - \hat{N}_{k\,k-ryt}\right]}{\left[\hat{M}_k - \hat{N}_{k\,k-ryt}\right] - \left[S_{mk} - S_{kk-ryt}\right] - \left[\hat{M}_{k+1} - \hat{N}_{k+1\,k-ryt}' - (\hat{N}_{k+1\,k} + \hat{N}_{k+1\,ky})\right]} =$$

$$\frac{(1 - \hat{A}_{k-1})}{(1 - \hat{P}_k)(1 - \hat{A}_k)\,\hat{A}_{k-1}} \quad ,$$

for k = r, ---, (ℓ-1).

The numerator of (A17) can be described as follows. The first term is the number of marked just after the (k-1)'th sample. The second term are those marked adults at time k except for those 'r' year old adults who have just arrived, and therefore were not among the marked adults at time (k-1). The difference then is the number of marked adults that did not survive to time k. Divided by an appropriate quantity, this will estimate the probability of dying before time k, (1-A(k)).

In the denominator, the first term are those adults who have survived from time (k-1) corrected for the 'r' year old adults just arriving. From these are removed those marked individuals who were in the k'th sample, again correcting for the 'r' year olds (Sm(k) - S(k,k-r,y,t)). The denominator now describes a certain group of marked adults who were not captured at time k. After accounting for the 'r' year old adults at time k and the marked adults that were captured at time k, the third term removes those marked adults that survived to time (k+1). The quantity then left in the denominator divided by an appropiate term estimates the compound probability in the right hand side; that is 'survives to time (k-1)' and 'is not captured at time k' and 'does not survive to time (k+1)'.

Using (A2) for $\hat{A}(k-1)$ and $\hat{A}(k)$ and (A6) for $\hat{P}(k)$, the right hand side of (A17) becomes:

$$\frac{(\tilde{M}_{k-1} + S_{k-10} - \tilde{M}_k + \hat{N}_{k\,k-ryt}) \cdot (\hat{M}_k + S_{ko}) \cdot \hat{M}_k}{(\hat{M}_k + S_{ko} - \tilde{M}_{k+1} + \hat{N}_{k+1\,k+1-ryt}) \cdot (\tilde{M}_k - \hat{N}_{k\,k-ryt}) \cdot (\tilde{M}_k - S_{mk})}$$

Using this form of the right hand side and rearranging, (A17) becomes:

$$\hat{N}_{k+1\,k} + \hat{N}_{k+1\,ky} = \left[\frac{\hat{M}_{k+1} - \hat{N}_{k+1\,k+1-ryt}}{\hat{M}_k + S_{ko}}\right] \cdot \left[S_{mk} + S_{ko} + \frac{\hat{N}_{k\,k-ryt}(\hat{M}_k - S_{mk})}{\hat{M}_k}\right] -$$

$$\left[\frac{\tilde{M}_k S_{k\,k-ryt} - S_{mk} \hat{N}_{k\,k-ryt}}{\hat{M}_k}\right] - N_{k+1\,k-ryt}' \quad ,$$

for $k = r, \dots, (\ell-1)$.

This is then simplified further, by substituting with the estimates given in equations (10), (A2), (A5) and (A6), to:

(A18) $\hat{N}_{k+1\,k} + \hat{N}_{k+1\,ky} = \hat{A}_k (S_{mk} + S_{ko})$,

for $k = r, \dots, (\ell-1)$.

This simple equation equates the estimated survival rate to the estimated proportion of the marked animals released from the k'th sample that have survived to time (k+1).

The last step in finding maximum likelihood estimates will be to establish recursive relations for the N(i,j,w) and the N(i,j,y,w). From these an estimate for M(i) will be extracted which will be applied in the necessary equations developed earlier on.

With k set to (1+1) in (8), the likelihood function of N(1+1,j,w) becomes:

$$L(N_{\ell+1jw}) = \frac{K \; A_\ell^{N_{\ell+1jw}} (1-A_\ell)^{N_{\ell+1j\omega}}}{N_{\ell+1jw}! \; (N_{\ell j\omega} - S_{\ell j\bar{\omega}} - N_{\ell+1j\nu})!} \quad ,$$

for $j = 1, \cdots, (\ell-1)$.

For large N(1+1,j,w), setting $\triangle$ in L(N(1+1,j,w)) to zero, gives, after summing over the capture histories w:

$$\frac{\hat{N}_{\ell j} - S_{\ell j}}{\hat{N}_{1+1j}} = \frac{1}{\hat{A}_\ell} \quad ,$$

for $j = 1, \cdots, (\ell-1)$

and rearranging

$$(A19) \quad (1-\hat{A}_\ell) = \frac{\hat{N}_{\ell j} - S_{\ell j} - \hat{N}_{\ell+1j}}{\hat{N}_{\ell j} - S_{\ell j}} \quad ,$$

for $j = 1, \cdots, (\ell-1)$.

Setting k = 1 and rearranging, equation (A12) becomes:

$$\left[\hat{N}_{\ell-1j} - S_{\ell-1j} - \hat{N}_{\ell j}\right] = \frac{(1-\hat{A}_{\ell-1})}{(1-\hat{P}_\ell)(1-\hat{A}_\ell)\hat{A}_{\ell-1}}\left[\hat{N}_{\ell j} - S_{\ell j} - \hat{N}_{\ell+1j}\right] \quad ,$$

for $j = 1, \cdots, (\ell-2)$.

Then using (A19) in the right hand side and multiplying both sides by

$$(1-\hat{P}_\ell)\hat{A}_{\ell-1}$$

and adding

$$(1-\hat{A}_{\ell-1})\left[\hat{N}_{\ell-1j} - S_{\ell-1j} - \hat{N}_{\ell j}\right]$$

to both sides results in:

(A20) $\left[\hat{N}_{\ell-1j} - S_{\ell-1j} - \hat{N}_{\ell j}\right] =$

$$\frac{(1-\hat{A}_{\ell-1})}{(1 - \hat{P}_\ell \hat{A}_{\ell-1})}\left[\hat{N}_{\ell-1j} - S_{\ell-1j} - S_{\ell j}\right] \quad ,$$

for $j = 1, \cdots, (\ell-2)$.

With $k=(l-1)$, (A12) now becomes:

$$\left[\hat{N}_{\ell-2j} - S_{\ell-2j} - \hat{N}_{\ell-1j}\right] = \frac{(1-\hat{A}_{\ell-2})}{(1-\hat{P}_{\ell-1})(1-\hat{A}_{\ell-1})\hat{A}_{\ell-2}}\left[\hat{N}_{\ell-1j} - S_{\ell-1j} - \hat{N}_{\ell j}\right],$$

for $j = 1, \cdots, (\ell-3)$.

Using (A20) for the right hand side leaves:

$$\left[\hat{N}_{\ell-2j} - S_{\ell-2} - \hat{N}_{\ell-1j}\right] = \frac{(1-\hat{A}_{\ell-2})}{(1-\hat{P}_{\ell-1})\,\hat{A}_{\ell-2}\,(1-\hat{P}_\ell\,\hat{A}_{\ell-1})}\left[\hat{N}_{\ell-1j} - S_{\ell-1j} - S_{\ell j}\right] \; ,$$

for $j = 1, \cdots, (\ell-3)$.

Multiplying both sides by

$$(1-\hat{P}_{\ell-1})\,\hat{A}_{\ell-2}\,(1-\hat{P}_\ell\,\hat{A}_{\ell-1})$$

then adding

$$(1-\hat{A}_{\ell-2})\left[\hat{N}_{\ell-2j} - S_{\ell-2j} - \hat{N}_{\ell-1j}\right]$$

gives the result:

$$\left[\hat{N}_{\ell-2j} - S_{\ell-2j} - \hat{N}_{\ell-1j}\right] =$$

$$\frac{(1-\hat{A}_{\ell-2})}{\left[(1-\hat{P}_{\ell-1})(1-\hat{P}_\ell\,\hat{A}_{\ell-1})\,\hat{A}_{\ell-2} + (1-\hat{A}_{\ell-2})\right]}\left[\hat{N}_{\ell-2j} - S_{\ell-2j} - S_{\ell-1j} - S_{\ell j}\right] \; ,$$
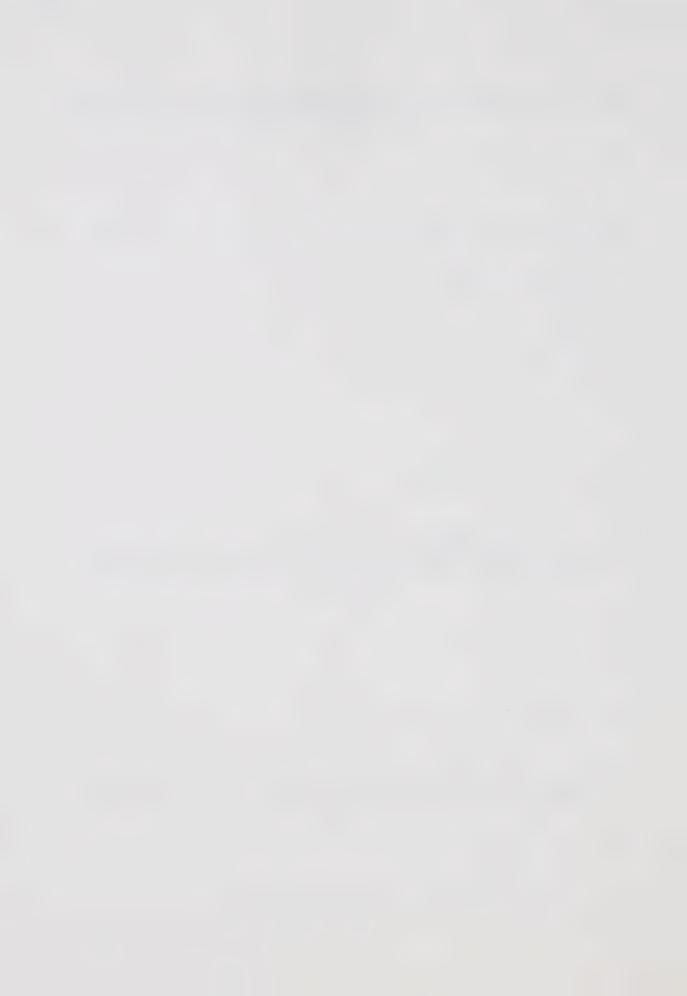
for $j = 1, \cdots, (\ell-3)$

which simplifies to:

$$(A21) \quad \left[\hat{N}_{\ell-2j} - S_{\ell-2j} - \hat{N}_{\ell-1j}\right] =$$

$$\frac{(1-\hat{A}_{\ell-2})}{1 - \hat{A}_{\ell-2}\left[1 - (1-\hat{P}_{\ell-1})(1-\hat{P}_\ell\,\hat{A}_{\ell-1})\right]}\left[\hat{N}_{\ell-2j} - S_{\ell-2j} - S_{\ell-1j} - S_{\ell j}\right] \; ,$$

for $j = 1, \cdots, (\ell-3)$.

So from (A20) and (A21) we have in general:

$$(A22) \quad \left[\hat{N}_{ij} - S_{ij} - \hat{N}_{i+1\,j} \right] = \frac{(1 - \hat{A}_i)}{\hat{\chi}_i} \left[N_{ij} - \sum_{h=i}^{\ell} S_{hj} \right]$$

for $i = 1, \ldots, \ell$ and $j = 1, \ldots, (i-1)$

where $\hat{\chi}_\ell = 1$ and $\hat{\chi}_i = 1 - \hat{A}_i \left[1 - (1 - \hat{P}_{i+1}) \hat{\chi}_{i+1} \right]$,

for $i = 1, \ldots, \ell$.

In (A22), written as

$$\frac{\left[\hat{N}_{ij} - S_{ij} - \hat{N}_{i+1\,j} \right]}{\left[\hat{N}_{ij} - \sum_{h=i}^{\ell} S_{hj} \right]} = \frac{(1 - \hat{A}_i)}{\hat{\chi}_i}$$

the numerator of the left side counts all those adults at time i last captured at time j who did not survive to time (i+1), analogous to the numerator of the right side, the probability of dying before time (i+1). The S(i,j) must be removed as they are no longer members of the N(i,j), after capture they become members of N(i+1,i). The denominator, meanwhile removes from the N(i,j) all those who were subsequently recaptured at some time up to time 1. This leaves the number of the N(i,j)'s which are never recaptured. Again, divided by N(i,j), this gives an estimate

of X(i), the probability of not being captured after time i.

Again, with k=(1+1) (8) contains the likelihood
function:

$$L(N_{\ell+1jyv}) = \frac{K \quad A_\ell^{N_{\ell+1jyv}} (1 - A_\ell)^{N_{\ell+1jyv}}}{N_{\ell+1jyv}! \ (N_{\ell jyw} - S_{\ell jyw} - N_{\ell+1jyv})!}$$,

for $j = 1, \cdots, (\ell-1)$.

For large N(1+1,j,y,v), equating the first difference of the
logarithm of this function to zero gives:

(A23) $\quad \dfrac{\hat{N}_{\ell jyw} - S_{\ell jyw}}{\hat{N}_{\ell+1jyv}} \quad = \quad \dfrac{1}{\hat{A}_\ell}$,

for $j = 1, \cdots, (\ell-1)$ except for $j = (\ell+1-r)$ when $w = t$.

Summing (A23) over all capture histories, w, except for
w = t when j = (1+1-r) and j=(1-r) gives:

(A24) $\dfrac{\hat{N}_{\ell jy} - \hat{N}_{\ell\ell-ryt} - S_{\ell jy} + S_{\ell\ell-ryt}}{\hat{N}_{\ell+1jy} - \hat{N}_{\ell+1\,\ell+1-ryt} - \hat{N}_{\ell+1\ell-ryt'}} = \dfrac{1}{\hat{A}_\ell}$,

for $j = 1, \cdots, (\ell-1)$.

Also excluding the case when w=t'=(t;0) andj=(1-1-r):

$$(A25) \quad \frac{\left[\begin{array}{l} \hat{N}_{\ell jy} - \hat{N}_{\ell\ell-ry\,t} - \hat{N}_{\ell-1\,\ell-1-ry\,t} - \\ S_{\ell jy} - S_{\ell\ell-ry\,t} - S_{\ell-1\,\ell-1-ry\,t} \end{array} \right]}{\left[\begin{array}{l} \hat{N}_{\ell+1jy} - \hat{N}_{\ell+1\,\ell+1-ry\,t} - \\ \hat{N}_{\ell+1\,\ell-ry\,t'} - \hat{N}_{\ell+1\,\ell-1-ry\,t''} \end{array} \right]} \;=\; \frac{1}{\hat{A}_{\ell}} \quad ,$$

for $j = 1, \cdots, (\ell-1)$.

And the case w=t''=(t;0,0) and j=(1-2-r):

$$(A\,26) \quad \frac{\left[\begin{array}{l} \hat{N}_{\ell jy} - \hat{N}_{\ell\ell-ry\,t} - \hat{N}_{\ell\ell-1-ry\,t'} - \hat{N}_{\ell\ell-2-ry\,t''} - \\ S_{\ell jy} + S_{\ell\ell-ry\,t} + S_{\ell\ell-1-ry\,t'} + S_{\ell\ell-2-ry\,t''} \end{array} \right]}{\left[\begin{array}{l} \hat{N}_{\ell+1jy} - \hat{N}_{\ell+1\,\ell+1-ry\,t} - \hat{N}_{\ell+1\,\ell-ry\,t'} - \\ \hat{N}_{\ell+1\,\ell-1-ry\,t''} - \hat{N}_{\ell+1\,\ell-2-ry\,t''} \end{array} \right]} \;=\; \frac{1}{\hat{A}_{\ell}} \quad ,$$

for $j = 1, \cdots, (\ell-1)$.

These equations (A24), (A25) and (A26) will be used
successively to develop the recursive relation for the
N(i,j,y,w).

In equation (A10), let k=1 and sum over all capture
histories w, except for w=t when j=(1-r) which must be
excluded. When j=(1+1-r) and w=t the equation is present but
N(1+1,1+1-r,y,t) is never given as the last term in the

denominator in the left side (since all of the terms in the numerator in this case are zero) and so it must be excluded as well.

Thus (A10) may be written as:

$$\left[\hat{N}_{\ell-1jy} - S_{\ell-1jy} - \hat{N}_{\ell jy} + \hat{N}_{\ell\ell-ryt}\right] =$$

$$\frac{(1-\hat{A}_{\ell-1})}{(1-\hat{P}_{\ell})(1-\hat{A}_{\ell})\hat{A}_{\ell-1}} \left[\begin{array}{c}\hat{N}_{\ell jy} - S_{\ell jy} - \hat{N}_{\ell+1jy} + \hat{N}_{\ell+1\ell-1-ryt} - \\ \hat{N}_{\ell\ell-ryt} + S_{\ell\ell-ryt} + \hat{N}_{\ell+1\ell-ryt'}\end{array}\right]$$

Using (A24) in the right side, this becomes:

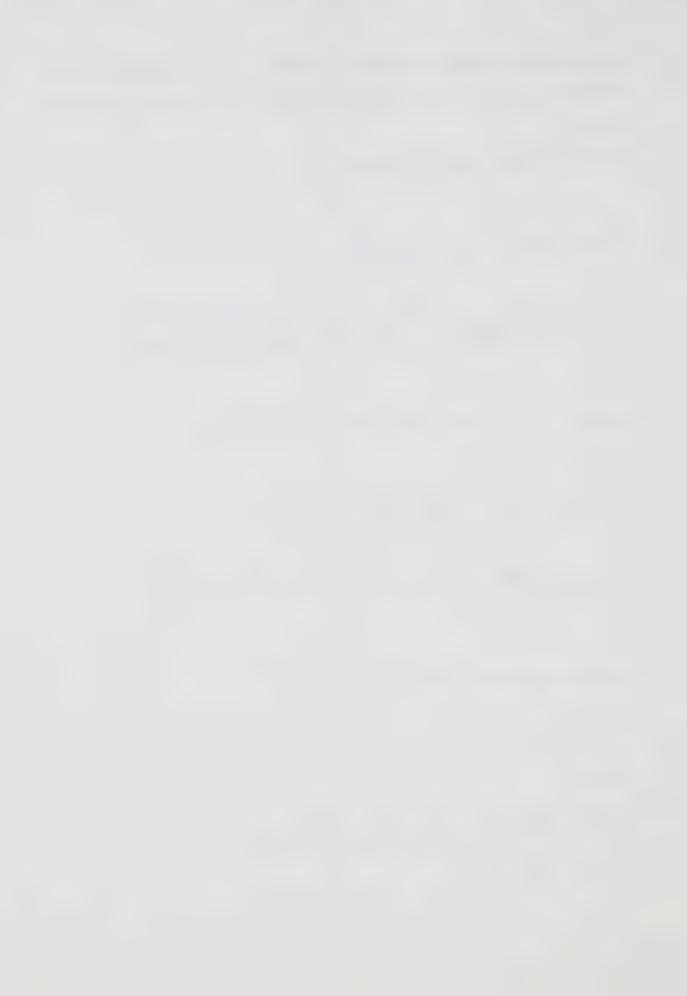$$\left[\hat{N}_{\ell-1jy} - S_{\ell-1jy} - \hat{N}_{\ell jy} + \hat{N}_{\ell\ell-ryt}\right] =$$

$$\frac{(1-\hat{A}_{\ell-1})}{(1-\hat{P}_{\ell})\hat{A}_{\ell-1}} \left[\hat{N}_{\ell jy} - \hat{N}_{\ell\ell-ryt} - S_{\ell jy} + S_{\ell\ell-ryt}\right]$$

Now multiply both sides by

$$(1-\hat{P}_{\ell})\hat{A}_{\ell-1}$$

and add

$$(1-\hat{A}_{\ell-1})\left[\hat{N}_{\ell-1jy} - S_{\ell-1jy} - \hat{N}_{\ell jy} + \hat{N}_{\ell\ell-ryt}\right]$$

to both sides. Thus:

(A27) $\left[\hat{N}_{\ell-1jy} - S_{\ell-1jy} - \hat{N}_{\ell jy} + \hat{N}_{\ell\ell-ryt} \right] =$

$$\frac{(1-\hat{A}_{\ell-1})}{(1-\hat{P}_\ell \hat{A}_{\ell-1})} \left[\hat{N}_{\ell-1jy} - S_{\ell-1jy} - S_{\ell jy} + S_{\ell\ell-ryt} \right] ,$$
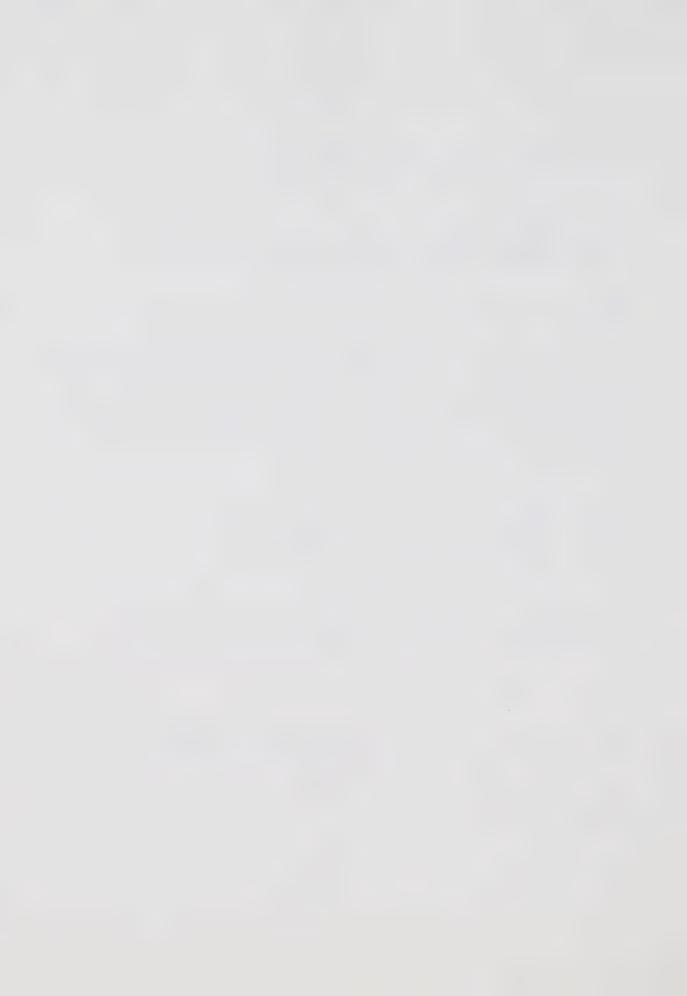
for $j = 1, \ldots, (\ell-2)$.

Let k=1 in (A10) as above but when summing over capture histories exclude the case w=t when j=(1-1-r) as well. By following the same sequence of steps that lead to (A27) and using (A25) in place of (A24) we have:

(A28) $\left[\begin{array}{l} \hat{N}_{\ell-1jy} - S_{\ell-1jy} - \hat{N}_{\ell jy} + \hat{N}_{\ell\ell-ryt} \\ \hat{N}_{\ell-1\,\ell-1-ryt} + S_{\ell-1\ell-1-ryt} + \hat{N}_{\ell\ell-1-ryt'} \end{array} \right] =$

$$\frac{(1-\hat{A}_{\ell-1})}{(1-\hat{P}_\ell \hat{A}_{\ell-1})} \left[\begin{array}{l} \hat{N}_{\ell-1jy} - S_{\ell-1jy} - S_{\ell jy} + S_{\ell\ell-ryt} + \\ S_{\ell\ell-1-ryt'} + S_{\ell-1\ell-1-ryt} - \hat{N}_{\ell-1\ell-1-ryt} \end{array} \right] ,$$

for $j = 1, \ldots, (\ell-2)$.

Now let k=(1-1) in (A10) and exclude the mandatory j=(1-r) and j=(1-1-r) when w=t, when summing over the capture histories. Thus:

$$\left[\hat{N}_{\ell-2jy} - S_{\ell-2jy} - \hat{N}_{\ell-1jy} + \hat{N}_{\ell-1\ell-1-ryt} \right] =$$

$$\frac{(1 - \hat{A}_{\ell-2})}{(1 - \hat{P}_{\ell-1})(1 - \hat{A}_{\ell-1})\hat{A}_{\ell-2}} \left[\begin{array}{l} \tilde{N}_{\ell-1jy} - S_{\ell-1jy} - \hat{N}_{\ell jy} + \hat{N}_{\ell\ell-ryt} - \\ \hat{N}_{\ell-1\ell-1-ryt} + S_{\ell-1\ell-1-ryt} + \hat{N}_{\ell\ell-1-ryt'} \end{array} \right],$$
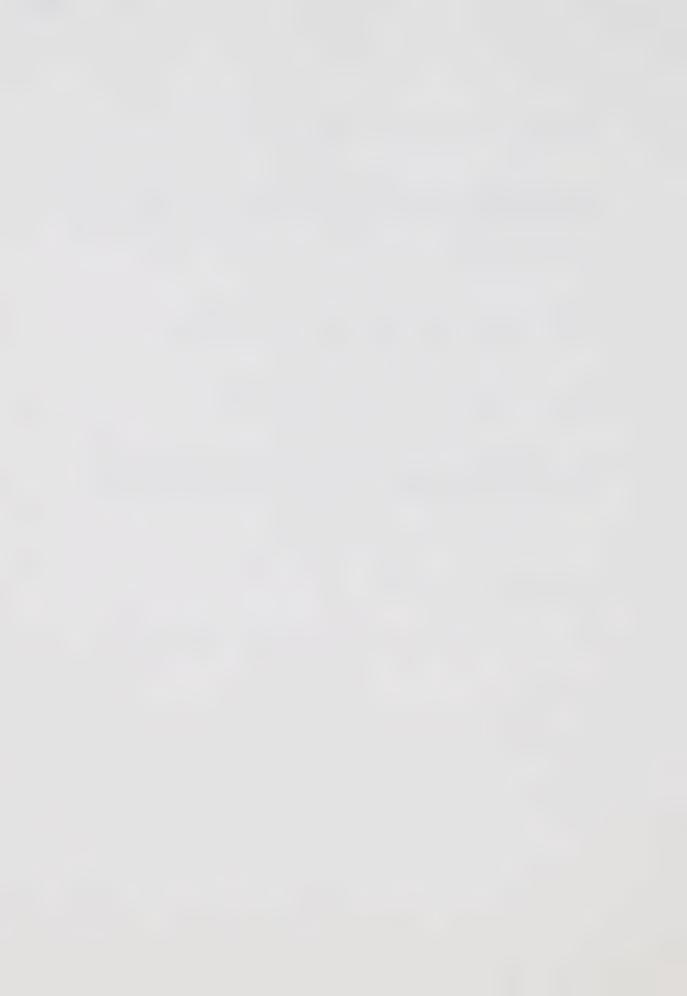
for $j = 1, \cdots, (\ell-3)$.

By using (A28) as the right side this becomes:

$$\left[\hat{N}_{\ell-2jy} - S_{\ell-2jy} - \hat{N}_{\ell-1jy} + \hat{N}_{\ell-1\ell-1-ryt} \right] =$$

$$\frac{(1 - \hat{A}_{\ell-2})}{(1 - \hat{P}_{\ell-1})(1 - \hat{P}_{\ell}\hat{A}_{\ell-1})\hat{A}_{\ell-2}} \left[\begin{array}{l} \hat{N}_{\ell-1jy} - S_{\ell-1jy} - S_{\ell jy} - S_{\ell\ell-ryt} + \\ S_{\ell\ell-1-ryt'} + S_{\ell-1\ell-1-ryt} - \hat{N}_{\ell\ell-1-ryt'} \end{array} \right]$$

Multiplying both sides by

$$(1 - \hat{P}_{\ell-1})(1 - \hat{P}_{\ell}\hat{A}_{\ell-1})\hat{A}_{\ell-2}$$

and adding

$$(1 - \hat{A}_{\ell-2}) \left[\hat{N}_{\ell-2jy} - S_{\ell-2jy} - \hat{N}_{\ell-1jy} + \hat{N}_{\ell-1\ell-1-ryt} \right]$$

results in:

$$(A29) \quad \left[\hat{N}_{\ell-2jy} - S_{\ell-2jy} - \hat{N}_{\ell-1jy} + \hat{N}_{\ell-1\,\ell-1-ryt} \right] =$$

$$\frac{(1-\hat{A}_{\ell-2})}{(1-\hat{P}_{\ell-1})(1-\hat{P}_\ell \hat{A}_{\ell-1})\hat{A}_{\ell-2} + (1-\hat{A}_{\ell-2})} \left[\begin{array}{l} \hat{N}_{\ell-2jy} - S_{\ell-2jy} - S_{\ell-1jy} - S_{\ell jy} + \\ S_{\ell\ell-ryt} + S_{\ell\,\ell-1-ryt'} + S_{\ell-1\,\ell-1-ryt} \end{array} \right],$$

for $j = 1, \ldots, (\ell-3)$.

Similarily by using (A26) and the appropriate forms of (A10), one gets for $k=(1-2)$:

$$(A30) \quad \left[\hat{N}_{\ell-3jy} - S_{\ell-3jy} - \hat{N}_{\ell-2jy} + \hat{N}_{\ell-2\,\ell-2-ryt} \right] =$$

$$\left[\frac{(1-\hat{A}_{\ell-3})}{(1-\hat{P}_{\ell-2})\left[(1-\hat{P}_{\ell-1})(1-\hat{P}_\ell \hat{A}_{\ell-1})\hat{A}_{\ell-2} + (1-\hat{A}_{\ell-2})\right]\hat{A}_{\ell-3} + (1-\hat{A}_{\ell-3})} \right] \times$$

$$\left[\begin{array}{l} \hat{N}_{\ell-3jy} - S_{\ell-3jy} - S_{\ell-2jy} - S_{\ell-1jy} - S_{\ell jy} + S_{\ell-2\,\ell-2-ryt} + \\ S_{\ell-1\,\ell-1-ryt} + S_{\ell-1\,\ell-2-ryt'} + S_{\ell\ell-ryt} + S_{\ell\ell-1-ryt'} + S_{\ell\ell-2-ryt''} \end{array} \right],$$

for $j = 1, \ldots, (\ell-4)$.

From the three equations (A27), (A29) and (A30) it easily seen that in general:

$$(A31) \quad \left[\hat{N}_{ijy} - S_{ijy} - \hat{N}_{i+1jy} + \hat{N}_{i+1\ i+1-ry\underline{t}} \right] =$$

$$\frac{(1 - \hat{A}_i)}{\hat{\chi}_i} \left[\hat{N}_{ijy} - S_{ijy} - \sum_{h=i+1}^{\ell} S_{hjy} + \sum_{k=i+1}^{i+r-1} \sum_{h=k}^{\ell} S_{h\ k-ry\underline{t}'} \right]$$

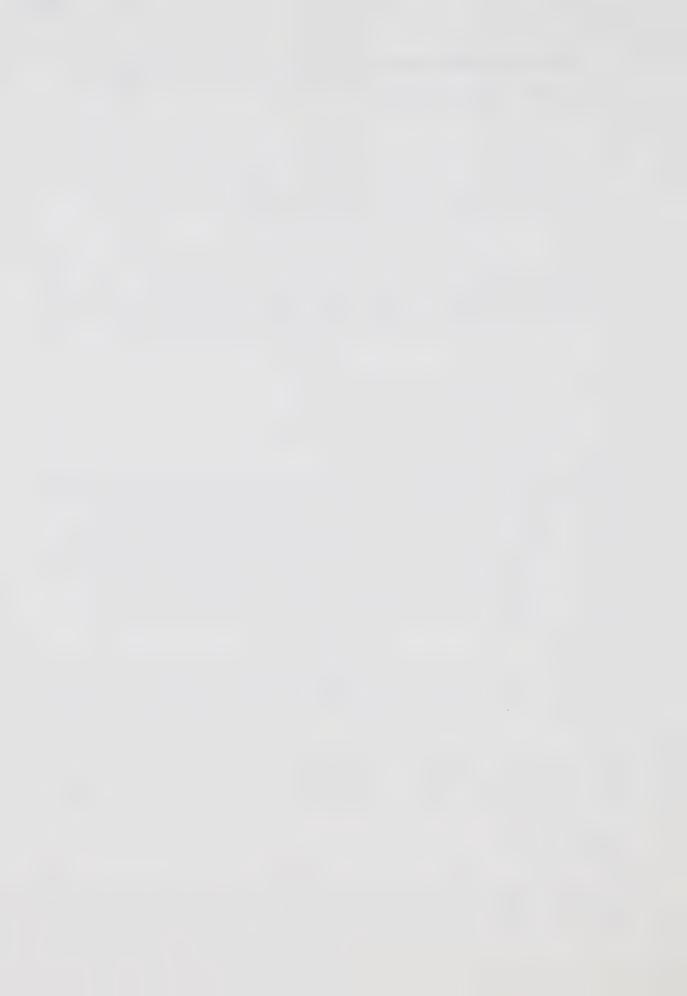$for\ i = 1, \cdots, (\ell-1)\ and\ j = 1, \cdots, (i-1).$

where $t' = (t;\ (h-k)\ zero's)$.

Intuitively this equation for adults marked as young is the same as that derived earlier for adults marked as adults (A22) with one change. The final sum in the right hand side of (A31) removes all of those individuals who were still young at time i and as a result could not be in the i'th sampling.

(A22) and (A31) are now summed together over all j such that j=1, ... ,(i-1). Thus:

$$\left[\sum_{j=1}^{i-1} (\hat{N}_{ij} + \hat{N}_{ijy}) - \sum_{j=1}^{i-1} (S_{ij} + S_{ijy}) - \sum_{j=1}^{i-1} (\hat{N}_{i+1j} + \hat{N}_{i+1jy}) + \hat{N}_{i+1\ i+1-ry\underline{t}} \right] =$$

$$\frac{(1 - \hat{A}_i)}{\hat{\chi}_i} \quad X$$

$$\left[\sum_{j=1}^{i-1} (\hat{N}_{ij} + \hat{N}_{ijy}) - \sum_{j=1}^{i-1} (S_{ij} + S_{ijy}) - \sum_{j=1}^{i-1} \sum_{h=i+1}^{\ell} (S_{hj} + S_{hjy}) - \sum_{k=i+1}^{i+r-1} \sum_{h=k}^{\ell} S_{h\ k-ry\underline{t}'} \right]$$

Which is further reduced, by using (1) and (2), to:

$$\left[\hat{M}_i - S_{mi} - \hat{M}_{i+1} + \hat{N}_{i+1\,i} + \hat{N}_{i+1\,iy} + \hat{N}_{i+1\,i+1-ry\,t} \right] =$$

$$\frac{(1-\hat{A}_i)}{\hat{\chi}_i} \left[\hat{M}_i - S_{mi} - Z_i \right]$$

Substituting for (A2) and (A18) in the left hand side, this simplifies to:

(A32) $\qquad \left[\hat{M}_i - S_{mi} \right] = \dfrac{Z_i}{(1-\hat{\chi}_i)}$,

for $i = r, \ldots, (\ell - r)$,

where

$$Z_i = \sum_{j=1}^{i-1} \sum_{h=i+1}^{\ell} (S_{hj} + S_{hjy}) - \sum_{k=j+1}^{i+r-1} \sum_{h=k}^{\ell} S_{h\,k-ry\,t'}$$

Since

$$\hat{\chi}_i = 1 - \hat{A}_i \left[1 - (1-\hat{P}_{i+1}) \hat{\chi}_{i+1} \right] ,$$

for $i = 1, \ldots, \ell$

then

$$(1 - \hat{\chi}_i) = \tilde{A}_i \left[\hat{P}_{i+1} + (1 - \hat{P}_{i+1})(1 - \hat{\chi}_{i+1}) \right] ,$$

for $i = 1, \ldots, \ell$.

Using (A2), (A6) and (A32) for $\hat{A}(i)$, $\hat{P}(i+1)$ and $(1 - \hat{X}(i+1))$ it follows that:

$$(1 - \hat{\chi}_i) = \left[\frac{\tilde{M}_{i+1} - \hat{N}_{i+1\,i+1-ryt}}{\tilde{M}_i + S_{io}} \right] \cdot \left[\frac{S_{mi+1}}{\hat{M}_{i+1}} + \left(1 - \frac{S_{mi+1}}{\hat{M}_{i+1}} \right) \frac{Z_{i+1}}{\hat{M}_{i+1} + S_{mi+1}} \right]$$

$$= \left[\frac{\hat{M}_{i+1} - \hat{N}_{i+1\,i+1-ryt}}{\hat{M}_i + S_{io}} \right] \cdot \left[\frac{S_{mi+1} + Z_{i+1}}{\hat{M}_{i+1}} \right]$$

Since, by excluding those which were r years old at time $(i+1)$,

$$(A33) \quad \frac{S_{mi+1} + Z_{i+1}}{\hat{M}_{i+1}} = \frac{S_{mi+1} + Z_{i+1} - \sum\limits_{h=i+1}^{\ell} S_{h\,i+1-ryt'}}{\hat{M}_{i+1} - \hat{N}_{i+1\,i+1-ryt}}$$

then

$$(1 - \hat{\chi}_i) = \frac{S_{mi+1} + Z_{i+1} - \sum\limits_{h=i+1}^{\ell} S_{h\,i+1-ryt'}}{\hat{M}_i + S_{io}}$$

But from equation (A32)

$$\frac{Z_i}{\hat{M}_i - S_{mi}} = (1 - \hat{X}_i) = \frac{S_{mi+1} + Z_{i+1} - \sum_{h=i+1}^{\ell} S_{hi+1-ry\ell'}}{\hat{M}_i + S_{io}}$$

From this the estimate for M(i) is:

$$(A34) \quad \tilde{M}_i = Z_i \left\{ \frac{S_{io}}{S_{mi+1} + Z_{i+1} - Z_i - \sum_{h=i+1}^{\ell} S_{hi+1-ry\ell'}} \right\} +$$

$$S_{mi} \left\{ \frac{S_{mi+1} + Z_{i+1} - \sum_{h=i+1}^{\ell} S_{hi+1-ry\ell'}}{S_{mi+1} + Z_{i+1} - Z_i - \sum_{h=i+1}^{\ell} S_{hi+1-ry\ell'}} \right\} \quad ,$$
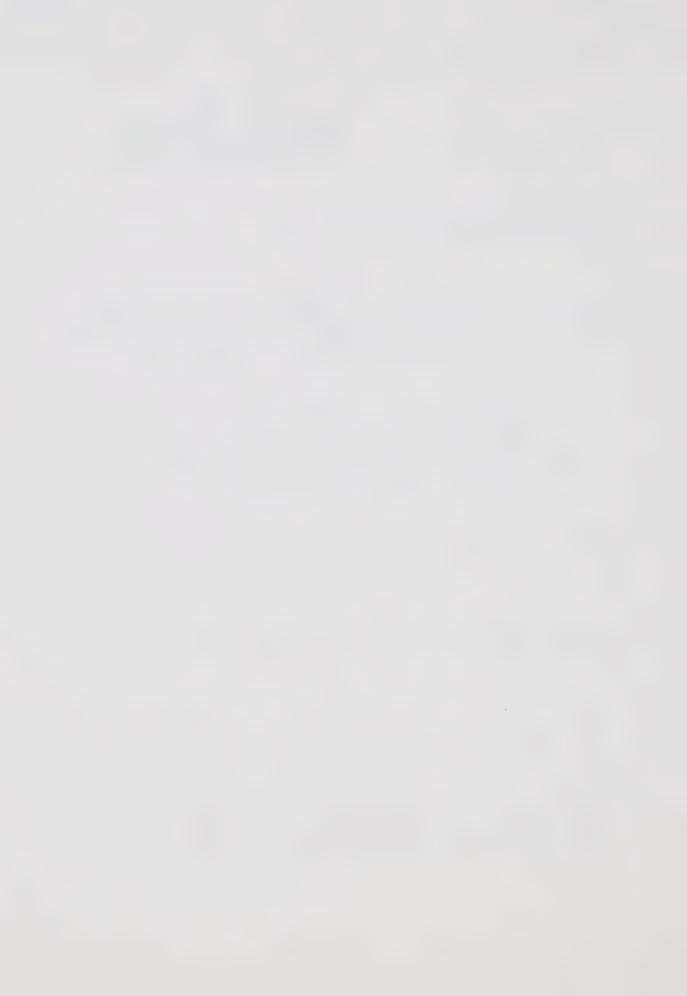
for $i = r, \ldots, (\ell-r)$.

Now

$$\left[S_{mi+1} + Z_{i+1} - Z_i - \sum_{h=i+1}^{\ell} S_{hi+1-ry\ell'} \right] =$$

$$\sum_{j=1}^{i} (S_{i+1j} + S_{i+1jy}) + \left[\sum_{j=1}^{i} \sum_{h=i+2}^{\ell} (S_{hj} + S_{hjy}) - \sum_{k=i+2}^{i+r} \sum_{h=k}^{\ell} S_{hk-ry\ell'} \right] -$$

$$\left[\sum_{j=1}^{i-1} \sum_{h=i+1}^{\ell} (S_{hj} + S_{hjy}) + \sum_{k=i+1}^{i+r-1} \sum_{h=k}^{\ell} S_{hk-ry\ell'} \right] - \sum_{h=i+1}^{\ell} S_{hi+1-ry\ell'}$$

Upon rearranging the limits of these summations this becomes:

$$\sum_{h=i+1}^{\ell} (S_{hi} + S_{hiy}) \ - \ \sum_{h=i+r}^{\ell} S_{hiyt'}$$

which is R(i).

So from (A34)

$$\hat{M}_i \ = \ Z_i \frac{S_{io}}{R_i} \ + \ S_{mi} \frac{(R_i + Z_i)}{R_i}$$

and

$$(A35) \qquad \hat{M}_i \ = \ \frac{Z_i}{R_i} (S_{io} + S_{mi}) \ + \ S_{mi} \quad ,$$

$$i = r, \ldots, (\ell - r).$$

Now from (A35), with (i+1) set to k:

$$\frac{S_{mk} + Z_k}{\hat{M}_k} \ = \ \frac{S_{mk} + Z_k - \displaystyle\sum_{h=k}^{\ell} S_{hk-ryt'}}{\hat{M}_k - \hat{N}_{kk-ryt}}$$

and so the estimate for the number of 'r' year old adults present in the population at time k becomes:

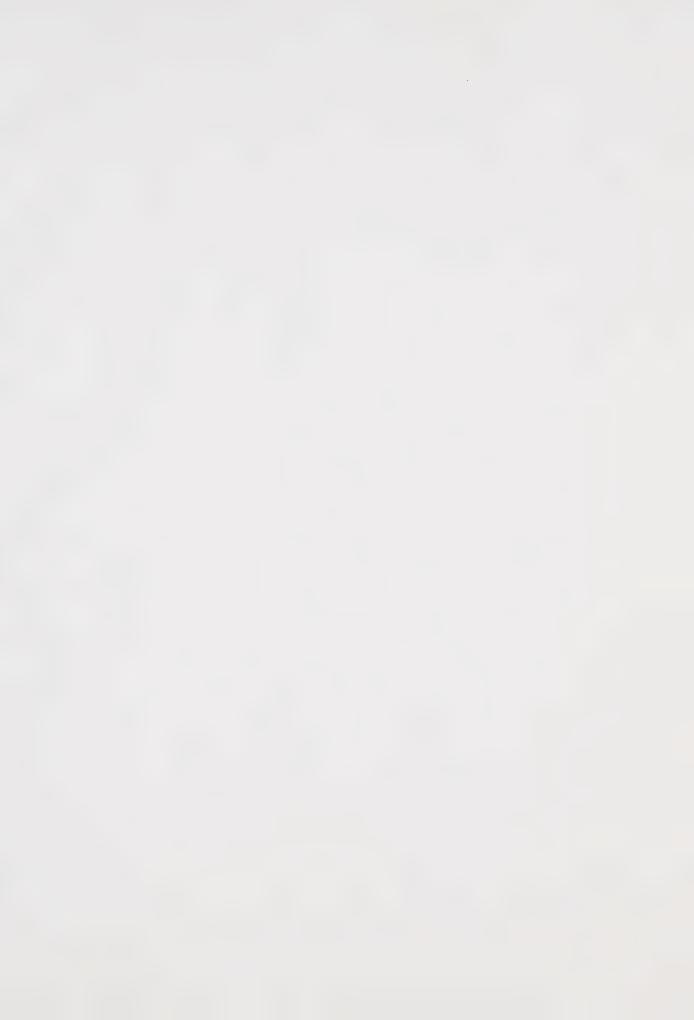$$(A36) \quad \hat{N}_{k\,k-ry\,t} = \hat{M}_k \frac{\sum_{h=k}^{\ell} S_{h\,k-ry\,t'}}{S_{mk} + Z_k} \quad ,$$

for $k = (r+1), \cdots, (\ell - r)$.

The denominator of (A36) counts all of those individuals which, captured in or prior to, the k'th sample are subsequently recaptured. The summation in the numerator tallies the individuals which were in the (k-r)'th sample as young (and are thus 'r' year old adults at time k) and are next seen in some k or later sample. Thus the expression, $\sum_{h=k}^{\ell} S(h,k-r,y,t') \Big/ \Big[Sm(k) + Z(k) \Big]$ represents the proportion of individuals subsequently recaptured, that are 'r' years old at time k. This proportion of the marked animals, M(k), yields the desired estimate.

This completes the estimation portion of this thesis. The remaining estimates are found by substituting into the previous equations the estimates for M(k) and N(k,k-r,y,t).

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